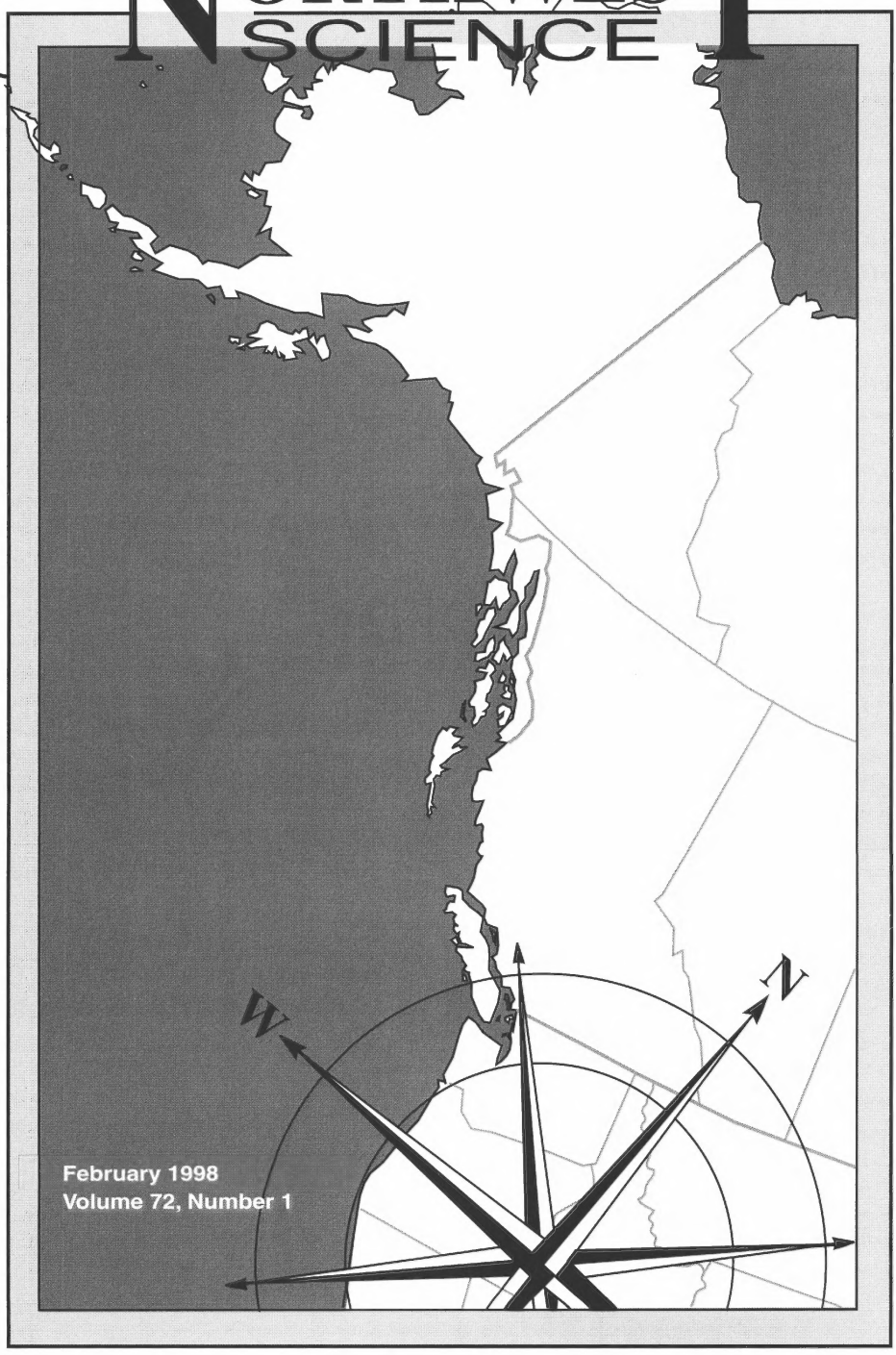
NORTHWEST SCIENCE



February 1998
Volume 72, Number 1

Northwest Scientific Association

(Founded 1923)

The Northwest Scientific Association, an affiliate of the American Association for the Advancement of Science, is an association representative of the basic and applied sciences and of social sciences.

Membership in the Northwest Scientific Association, which includes a subscription to *Northwest Science,* is open to individuals for $25 per year ($10 per year for students). Institutional membership, $40 per year. Sustaining membership, $40 per year for individuals and $100 per year for organizations, institutions, or agencies. Subscriptions are for the calendar year only.

Send change of address, payment of dues, or requests for undelivered issues to the Treasurer.

Editor of *Northwest Science*

David L. Peterson
Field Station for Protected Area Research
University of Washington, Box 352100
Seattle, Washington 98195
Telephone: 206-543-1587, Fax: 206-685-0790
Internet: wild@u.washington.edu

Officers of the Association

President Richard Cellarius
The Evergreen State College
Cheney, Washington (1998)

Past President Robert Carr
Eastern Washington University
Cheney, Washington

Secretary Margaret O'Connell
Department of Biology
Eastern Washington University
Cheney, Washington 99004

Treasurer David H. Hansen
Department of Biology
Pacific Lutheran University
Tacoma, Washington 98447 (1997)
Telephone: 206-535-7565
Fax: 206-536-5055
Internet: hansendh@plu.edu

*Term of office expires in the year given in parentheses.

Book Review Editor

Jerry O. Wolff
U.S. Environmental Protection Agency
200 SW 35th Street
Corvallis, Oregon 97333
Telephone: 541-754-4377, Fax: 541-754-4338
e-mail: wolffj@ccmail.orst.edu

Trustees:

Ross Black
Eastern Washington University
Cheney, Washington (1998)

Herbert Brown
Western Washington University
Bellingham, Washington (1999)

Miles Hemstrom
USDA Forest Service
Portland, Oregon (1999)

Barry L. Keller
Idaho State University
Pocatello, Idaho (1998)

John Koprowski
Willamette University
Salem, Oregon (2000)

Robin Matthews
Western Washington University
Bellingham, Washington (1998)

Paul A. McDaniel
University of Idaho
Moscow, Idaho (1997)

Kathy Ann Miller
University of Puget Sound
Tacoma, Washington (1998)

Margaret O'Connell
Eastern Washington University
Cheney, Washington (1999)

Kurt Othberg
Idaho Geological Survey
Moscow, Idaho (2000)

Michael D. Pitt
University of British Columbia
Vancouver, British Columbia (1998)

Tim Reynolds
Environmental Science and Research Foundation
Idaho Falls, Idaho (2000)

Roger Rosentreter
Bureau of Land Management
Boise, Idaho (1998)

Mark Sheehan
Washington Department of Natural Resources
Olympia, Washington (1998)

Theodore B. Thomas
USDI Fish & Wildlife Service
Olympia, Washinton (1999)

© 1998 by the Northwest Scientific Association. All rights reserved.

February 1998 Volume 72, Number 1

NORTHWEST SCIENCE

Editor	David L. Peterson	Field Station for Protected Area Research/University of Washington
Managing Editor	Nancy J. Grunewald	Washington State University
Indexer	Caroline Hooper	
Associate Editors		
Anthropology	R. Lee Lyman	University of Missouri—Columbia
Aquatic Biology	Gary L. Larson	U.S. Geological Survey—Corvallis
Botany	Eldon H. Franz	Washington State University
Mathematics & Computer Applications	Steven J. Ghan	Battelle Pacific Northwest Labs—Richland
Forestry	James K. Agee	University of Washington
Geology & Geography	David R. Gaylord	Washington State University
Soils	Robert L. Edmonds	University of Washington
Wildlife Biology	R. Gerald Wright	Cooperative Park Studies Unit/ University of Idaho
Zoology	Richard B. Forbes	Portland State University
Book Reviews	Jerry O. Wolff	U.S. EPA—Corvallis

ISSN #0029-344X

CONTENTS

Announcements

1 Burning Characteristics of Western Conifer Needles—**R.W. Fonda, L.A. Belanger, and L.L. Burley**

10 Relationships among Environmental Variables and Tree Species Distribution at High Elevations in the Olympic Mountains—**Andrea Woodward**

23 Antibacterial Activity of Two Species of Bryozoans from Northern Puget Sound—**Jill S. Shellenberger and June R.P. Ross**

34 Landscape Changes within the Historical Distribution of Columbian Sharp-tailed Grouse in Eastern Washington: Is There Hope?—**Matthew W. McDonald and Kerry P. Reese**

42 Reporting Scale and the Information Content of Streamflow Data—**Paul H. Whitfield**

Northwest Science Forum

52 Environmental Justice and Natural Resource Management in the Pacific Northwest—**Debra J. Salazar with Nicole Oliver**

Book Reviews

57 *Geographic Variation in Forest Trees: Genetic Basis and Application of Knowledge in Silviculture*, by E. Kristian Morgenstern — **reviewed by Steve Clements**

59 *Ecology and Management of Sitka Spruce, Emphasizing Its Natural Range in British Columbia*, by E.B. Peterson, N.M. Peterson, G.F. Weetman, and P.J. Martin — **reviewed by Steven A. Acker**

61 *Plant Dormancy: Physiology, Biochemistry and Molecular Biology*, by G.A. Lang (ed.)—**reviewed by James A. Weber**

63 *Macrolichens of the Pacific Northwest*, by Bruce McCune and Linda Geiser—**reviewed by Roger Rosentreter**

64 *Biodiversity II: Understanding and Protecting Our Biological Resources*, by Marjorie L. Reaka-Kudla, Don E. Wilson, and Edward O. Wilson (eds.)—**reviewed by Stephen Polasky**

66 *Red-winged Blackbirds: Decision-making and Reproductive Success*, by Les D. Beletsky and Gordon H. Orians—**reviewed by James N.M. Smith**

68 *Upstream: Salmon and Society in the Pacific Northwest*, by Committee on Protection and Management of Pacific Northwest Anadromous Salmonids—**reviewed by Robert T. Lackey**

70 *Fish Stress and Health in Aquaculture*, by G.K. Iwama et al. (eds.)—**reviewed by James L. Congleton**

72 *The Evolution of Social Behavior in Insects and Arachnids*, by Jae C. Choe and Bernard J. Crespi (eds.)—**reviewed by John Melville**

74 *The Evolution of Mating Systems in Insects and Arachnids*, by Jae C. Choe and Bernard J. Crespi (eds.)—**reviewed by Sara Tallarovic**

76 *Washington Forest Landscape Management Project—A Pragmatic, Ecological Approach to Small-Landscape Management*, by A.B. Carey et al.—**reviewed by Janet L. Ohmann**

78 *Economic Analysis of Forest Landscape Management Alternatives*, by Bruce R. Lippke, John Sessions, and Andrew B. Carey—**reviewed by Ralph J. Alig and Jeffrey Kline**

Index

Information for Authors

Reviewers of Manuscripts

Announcements

1998 Annual Meeting, The Evergreen State College, March 25-27

The 71st annual meeting of the Northwest Scientific Association will be hosted by The Evergreen State College at its campus near Olympia, Washington. The meetings will be held jointly with the Society for Northwestern Vertebrate Biology and the Lichen Guild on March 25-27, 1998. Following a business meeting of the Governing board on March 25, scientific sessions will occur on the following two days with a variety of concurrent sessions and symposia. Work is underway for symposia on rare plants, the USDA Forest Service DEMO project, and forest canopies. An opening plenary symposium on the interface between scientific research and governmental policy is under consideration. Field trips to ecological research sites on Fort Lewis, Northwest Trek Wildlife Park, and the Gifford Pinchot National Forest canopy crane site are also being planned.

Members of all the sponsoring groups as well as nonmembers are welcome at the meeting, and students are especially encouraged to attend and report the results of their research. The call for abstracts and registration information has been mailed to all members of the Association.

Information about the meeting may be obtained from Richard Cellarius, meeting chair, or Gabe Tucker, program chair, at The Evergreen State College, Olympia, WA 98505; e-mail address is nwsa@elwha.evergreen.edu. The address for accessing meeting information on the World Wide Web is http://www.evergreen.edu/nwsa98.

Associate Editor Changes

This is the last issue in which James K. Agee and R. Gerald Wright will appear in the editorial masthead of *Northwest Science*. Jim Agee has stepped down as Associate Editor for Forestry after serving the journal in this capacity for 11 years, and now serves as an Associate Editor for *Ecological Applications*. Gerry Wright has stepped down after six years of service as Associate Editor for Wildlife, and is the new Editor-in-Chief of *Biological Conservation*. These two Associate Editors have been among our busiest in terms of the number of manuscripts submitted. I appreciate their excellent assistance in the review process of *Northwest Science*, and wish them the best in their new ventures with other journals. New Associate Editors for Forestry and Wildlife will be announced in the next issue of *Northwest Science*.

—The Editor

R. W. Fonda, L. A. Belanger, and **L. L. Burley,** Department of Biology, Western Washington University, Bellingham, Washington, 98225

Burning Characteristics of Western Conifer Needles

Abstract

The needles from thirteen species of western conifers were burned to compare flammability of nonwoody fuels. The following burning characteristics were measured in a completely randomized design ANOVA: maximum flame height, flame time, ember time, burn time, percent combusted, and mean rate of weight loss. The burning characteristics tested in this study address important aspects of nonwoody fuel flammability in coniferous forests. Ponderosa pine, Jeffrey pine, Monterey pine, coast redwood, knobcone pine, giant sequoia, and sugar pine ranked in the upper half of most of the burn categories. These highly flammable species are prominent in communities for which fire return intervals are two to four decades. Lodgepole pine, western redcedar, Douglas-fir, Pacific silver fir, subalpine fir, and western hemlock seldom ranked in the upper half of any of the burn categories. The needles of these species are less flammable than the upper group of seven. The fire return intervals for the communities in which they grow are commonly two or more centuries.

Introduction

Most forest communities in Washington, Oregon, and California experience fire at some time in their developmental history. For some, the fire return interval (FRI) is about one to three decades, whereas for others the FRI is one to three or more centuries. Fire is a natural environmental factor affecting forest communities, but the effects of fire are determined by fuel loading, size class, arrangement, and chemical composition. These fuel characteristics are affected by other community characteristics.

When feedback from natural community characteristics limits the frequency, intensity, or severity of fire, the relationship may be considered homeostatic (*sensu* Odum 1969; e.g., fire-stable). Stability is a measure of homeostasis (Holling 1973), the ability of the component species to tolerate a disturbance and maintain the niche structure of the community. Forests that historically met the definition of fire-stable are characterized by: 1) short FRI (Agee 1993, Pyne et al. 1996); 2) species with highly flammable fuels because of fuel chemistry and low fuel moisture (Mutch 1970, Bond and Midgley 1995); 3) frequent ignition events from lightning (Komarek 1968, Keeley 1977, Agee 1994); 4) low intensity, low severity surface fires (Agee 1989); 5) species with fire-adaptive characteristics, allowing individual plants to survive the fire (Agee 1993, Pyne et al. 1996). Further reference to fire-stable forests in this paper are to historical fire regimes.

Ponderosa pine, Jeffrey pine, and giant sequoia dominate forests with fire-stable characteristics (Sweeney 1967, Vogl 1967, Weaver 1967, Kilgore 1972, Habeck and Mutch 1973, Kilgore and Taylor 1979, Arno 1980, Madany and West 1980, Bonnicksen and Stone 1982, Arno and Peterson 1983, Swetnam and Dieterich 1983, van Wagtendonk 1983, Agee et al. 1990, Swetnam 1993, Agee 1994). Sugar pine often exists as a subordinate member of fire-stable communities (Kilgore 1972; van Wagtendonk 1983; Thomas and Agee 1986).

Communities controlled by fire are not homeostatic with fire, but the individual species in the community still must respond to the disturbance. Resilience is a measure of persistence (Holling 1973, Fonda 1976, Westman and O'Leary 1986), the ability of the component species to persist on the site. Many species exist in forest communities that are involved with fire on a stand-replacing scale. Such fires often burn with high intensity and high severity (Agee 1993). Individual trees are killed by stand-replacing fires, yet the species persist on the site. Such forests, for which the prefire species return to the postfire site, are termed fire-resilient. Forests that historically met the definition of fire-resilient are characterized by: 1) long FRI (Agee 1993, Pyne et al. 1996); 2) species with less flammable fuels (Mutch 1970, Bond and Midgley 1995); 3) infrequent ignition events; 4) high intensity, moderate to high severity, stand-replacing fires (Agee 1989); 5) species that lack fire-adaptive characteristics and generally survive on the postfire site

© 1998 by the Northwest Scientific Association. All rights reserved.

by seed germination (Agee 1993; Pyne et al. 1996). Further reference to fire-resilient forests in this paper are to historical fire regimes.

Monterey pine, coast redwood, knobcone pine, lodgepole pine, Douglas-fir, and subalpine fir dominate forests with predominantly fire-resilient characteristics, although each forest type also has been known to support low intensity, low severity surface burns (Vogl 1967, 1973; Fonda and Bliss 1969; Vogl et al. 1977; Fonda 1976; Arno 1980; Romme and Knight 1981; Agee and Smith 1984; Stuart 1987; Finney and Martin 1989; Romme and Despain 1989; Agee et al. 1990; Greenlee and Langenheim 1990; Morrison and Swanson 1990; Taylor and Fonda 1990; Agee 1991, 1994; Brown and Swetnam 1994; Wetzel 1995).

Western redcedar, Pacific silver fir, and western hemlock are associated with forest types that burn infrequently, usually with high severity, stand-replacing fires (Fonda and Bliss 1969; Arno 1980; Hemstrom and Franklin 1982; Agee et al. 1990; Agee 1993, 1994).

Agee (1993) classified Pacific Northwest conifers according to the strategies by which they adapt to low severity fires (Table 1). Resisters generally dominate fire-stable communities, whereas the other strategies listed in Table 1 are adaptations for species that dominate fire-resilient communities, or are sensitive to fire at any age. Agee (1993) cautioned that researchers should be aware that most species cannot be classified according to merely one of these strategies. Tree species respond differently to fire, depending on tree age and fire severity. For instance, older trees of coast redwood, Douglas-fir, Monterey pine, and western redcedar can resist low severity fires (i.e., a fire-stable strategy), but perish as young trees or in high severity fires (i.e., a fire-resilient strategy).

In any community in which fire is an ecological factor, the fire must start and continue to burn. Four requirements must be met at the time of the fire: 1) flammable fuels; 2) sufficient fuel loads to carry the fire through the community; 3) low environmental moisture; 4) ignition sources.

In this work we focus on measures of flammable fuels, specifically nonwoody fuels from species associated with fire-stable and fire-resilient conifer forests (Table 1). Mutch (1970) burned nonwoody fuels to formulate a hypothesis that natural selection favored the development of highly flammable species that perpetuate the fire environment. Taylor and Fonda (1990) employed the methods used by Mutch (1970) to assess burning characteristics of fuels in subalpine fir forests on Hurricane Ridge in Olympic National Park. Because they burned reasonably intact samples of the litter layer that had accumulated on the forest floor, their litter layers mixed some woody fuels with the largely nonwoody fuels. To our knowledge, no other studies exist that tested burning characteristics of nonwoody fuels to describe their contribution to the fire status of forests.

We studied in a fire chamber burning characteristics of the needles from 13 conifer species from forests in Washington, Oregon, California, and Nevada as indicators of flammability. Flammability has four components: ignitability,

TABLE 1. Species sampled and collection sites. Botanical nomenclature follows Hickman (1993). The strategy used by mature trees to resist low severity fire is based on information provided in Agee (1993).

Common name	Latin name	Strategy	Collection site
Coast redwood	*Sequoia sempervirens*	Resister	J. P. Burns Park (Big Sur), CA
Douglas-fir	*Pseudotsuga menziesii*	Resister	Cascade Mountains (Wenatchee), WA
Giant sequoia	*Sequoiadendron gigantea*	Resister	Sequoia National Park (Giant Forest), CA
Jeffrey pine	*Pinus jeffreyi*	Resister	Carson Range (Lake Tahoe), NV
Knobcone pine	*Pinus attenuata*	Evader	Siskiyou Mountains (Cave Junction), OR
Lodgepole pine	*Pinus contorta*	Evader	Olympic National Park (Deer Park), WA
Monterey pine	*Pinus radiata*	Evader	Monterey Peninsula, CA
Pacific silver fir	*Abies amabilis*	Avoider	Cascade Mountains (Stevens Pass), WA
Ponderosa pine	*Pinus ponderosa*	Resister	Cascade Mountains (Roslyn), WA
Subalpine fir	*Abies lasiocarpa*	Avoider	Olympic National Park (Deer Park), WA
Sugar pine	*Pinus lambertiana*	Resister	Siskiyou Mountains (Cave Junction), OR
Western hemlock	*Tsuga heterophylla*	Avoider	Olympic Peninsula (Sappho), WA
Western redcedar	*Thuja plicata*	Avoider	Lake Padden Park (Bellingham), WA

combustibility (intensity), sustainability, and consumability (Martin et al. 1994). Our work relates to intensity (flame height), sustainability of the fire (flame time, ember time, and burn time), and consumability of the fuel (percent consumption and mean rate of weight loss). We sought answers to two research questions: 1) are differences in burning characteristics among the species significant? 2) how do these 13 species contribute to the fire environment of the communities in which they grow?

Methods

We followed the methods in Mutch (1970) and Taylor and Fonda (1990). The experiment was designed as a completely randomized design ANOVA, with the species constituting the 13 treatments. Significant differences among the species for each burning characteristic were determined by a Newman-Keuls multiple range test (Zar 1996). The significance level was set at 5% before testing began. The data for percent combusted were transformed by arcsin before analysis. We burned 10 samples of each species, for a total of 130 burns.

Species and collection sites are listed in Table 1. Needles from all species were gathered from nearly pure batches from several different locations at each site, then allowed to dry in the lab. Needles for the burn tests were separated from the forest debris and stray needles of other species mixed in the sample.

We used ~15-g samples of conifer needles in the test burns. Samples were placed in aluminum trays and dried at 103°C for 72 hr. Samples were removed from the ovens and allowed to equilibrate for 2-3 min, then weights were adjusted by removing needles until the sample to be burned weighed 15.0 to 15.3 g. Moisture content at time of burning was 1.5-2.7%.

The fire chamber was 1 m^2 by 3 m tall, with a four-story exhaust chimney. Excessive draw from the chimney over the fire bed was prevented by a series of baffles in the chimney, and air movement was controlled by a fan in the chimney. Mean air velocity equaled 9.96±0.9 cm sec^{-1}, based on 25 measurements using a Barnant Company Tri-Sense meter (Model 637-0000).

The fuel bed was arranged on the floor of the chamber in a 35 x 35 cm grid formed by eight strings dipped in xylene. All fuel beds were < 5 cm high. Strings were ignited, and two timers were started when fuels first ignited. Maximum flame height was judged by comparing the highest point reached by flames against a meter stick at the rear of the fire chamber. At this point, the room lights were extinguished so that we could judge flame and burn times.

The first timer was stopped when all flames were extinguished (= flame time). The second timer was stopped when the last ember was extinguished (= burn time). The difference between these two is ember time.

Percent fuel combusted was determined by weighing the ashes, after removing the unburned bits of string, then dividing consumed weight by initial weight. Mean rate of weight loss was calculated as mg lost over burn time.

The six categories shown in Table 2 were calculated from the burn data. Regardless of the results of the multiple range test (MRT), species were ranked in order from the top species (#1) to the bottom species (#13) for each category. For each species, we added the ranked values for each burning characteristic to create a single list of combined flammability ranks, as shown in Table 3. In our judgment, each characteristic contributes to the interpretation of fire effects in a forest, so that they have equal weights. The means of all treatments are provided in Table 2 for readers who wish to create their own ranking.

Results

Jeffrey pine had significantly higher flames than any other species, followed by ponderosa pine (Table 2). Means for both species exceeded 60 cm. Jeffrey pine had the four highest flames (87 cm max) of the 130 individual burns in this study. Maximum height for an individual ponderosa pine burn was 75 cm. The differences among coast redwood, Monterey pine, sugar pine, and knobcone pine were not significant, nor were the differences among lodgepole pine, giant sequoia, western redcedar, and Pacific silver fir. The flames for Douglas-fir and western hemlock (no significant difference) and subalpine fir were the shortest of the species tested. Subalpine fir had significantly shorter mean flame height than any other species. Maximum flame height for subalpine fir was 22 cm.

TABLE 2. Means of burning characteristics resulting from ten test burns for each species.

MAXIMUM FLAME HEIGHT (cm)

JP	PP	RW	MP	SP	KP	LP	GS	WRC	PSF	DF	WH	SAF
76.7	69.3	59.4	58.3	55.6	55.6	43.2	42.6	42.4	38.4	26.2	24.6	16.7

FLAME TIME (sec)

GS	SP	LP	WRC	DF	KP	PP	MP	SAF	PSF	RW	WH	JP
148.5	128.5	121.8	113.2	105.8	99.2	92.4	82.6	79.8	79.8	73.4	68.4	64.7

EMBER TIME (sec)

MP	JP	RW	GS	KP	PP	WRC	LP	SP	SAF	PSF	WH	DF
328.3	326.7	317.3	242.6	206.3	149.7	130.7	118.7	103.2	91.8	84.8	43.6	21.8

BURN TIME (sec)

MP	JP	RW	GS	KP	WRC	PP	LP	SP	SAF	PSF	DF	WH
410.9	391.4	390.8	386.1	305.6	243.9	242.1	240.5	231.8	171.6	164.6	127.6	112.1

% COMBUSTED

PP	JP	RW	MP	KP	SP	GS	LP	WRC	PSF	DF	SAF	WH
91.1	90.1	86.1	85.1	84.7	77.1	75.8	73.0	45.7	32.0	26.6	25.6	18.8

MEAN RATE OF WEIGHT LOSS (µg/sec)

PP	SP	LP	KP	JP	RW	DF	GS	MP	WRC	PSF	WH	SAF
58.2	50.9	49.3	42.0	35.3	33.5	31.6	30.4	30.3	29.9	29.4	26.8	23.4

Means connected by underline are not significantly different. Species abbreviations: DF = Douglas-fir; GS = giant sequoia; JP = Jeffrey pine; KP = knobcone pine; LP = lodgepole pine; MP = Monterey pine; PP = ponderosa pine; PSF = Pacific silver fir; RW = coast redwood; SAF = subalpine fir; SP = sugar pine; WH = western hemlock; WRC = western redcedar.

The flames for giant sequoia lasted significantly longer than any other species tested (Table 2). Four of the ten trials exceeded 160 sec, with a maximum of 187 sec. Otherwise, there was much overlap in the MRT for mean flame times, and the remaining species exhibited a continuum of times. There were no significant differences among the seven species with less than 95 sec mean flame time (ponderosa pine, Monterey pine, subalpine fir, Pacific silver fir, coast redwood, western hemlock, and Jeffrey pine).

Ember times for Monterey pine, Jeffrey pine, and coast redwood were not significantly different. Mean ember times for these species exceeded 300 sec (Table 2). Maximum ember times for individual burns for Jeffrey pine and coast redwood were 454 sec; for Monterey pine, 418 sec. This upper group was followed by giant sequoia and knobcone pine (not significantly different), for which mean ember times were in the 200 sec range. A large group, ranging from 84-150 sec includes ponderosa pine, western redcedar, lodgepole pine, sugar pine, subalpine fir, and Pacific silver fir. The maximum ember time for an individual burn for the species in this group was 242 sec (ponderosa pine). There were no significant differences between western hemlock and Douglas-fir, for which mean ember times were significantly shorter (< 50 sec) than any other species.

There were no significant differences in mean burn time among Monterey pine, Jeffrey pine, coast redwood, and giant sequoia, all of which had significantly longer mean burn times than the other nine species (Table 2). Each of the top species had at least three individual burns that exceeded 400 sec. Knobcone pine was significantly different from all other species, but shorter than the upper group. No knobcone pine burn exceeded 355 sec. Western redcedar, ponderosa pine, lodgepole pine, and subalpine fir composed the middle group, the means of which were in the mid-200 sec range. The group with the shortest burn times comprised subalpine fir, Pacific silver fir, Douglas-fir, and western hemlock. Mean burn times in this group were < 200 sec, significantly shorter than the other species. Maximum burn time among these four species was 203 sec (subalpine fir).

Mean percent fuel combusted was not significantly different between ponderosa pine and Jeffrey pine, both of which had greater values than any of the other species (Table 2). The minimum percent consumed for any individual burn for these two species was 87% (ponderosa pine). There were no significant differences among coast redwood, Monterey pine, and knobcone pine. Sugar pine and giant sequoia were not significantly different. The minimum single burn value among these five species was 65% (giant sequoia). Lodgepole pine lost >70% fuel, but ranked significantly below sugar pine and giant sequoia. Western hemlock had significantly less mean fuel combusted than any other species, and maximum fuel combusted for an individual western hemlock burn was 22%. Douglas-fir and subalpine fir (not significantly different) ranked just above western hemlock. Western redcedar and Pacific silver fir, both significantly different from other species, averaged less than 50% fuel combusted.

Ponderosa pine fuel was consumed at a significantly higher mean rate than any other species (Table 2). Ponderosa pine also produced the two highest individual rates (80 and 73 µg/sec). There were no significant differences among sugar pine and lodgepole pine, for which maximum individual rates were 62-63 µg/sec. Knobcone pine was the fifth species to lose more than a mean of 40 µg/sec, with a maximum value of 46 µg/sec. The remaining species constitute a large group among which there was much overlap in the MRT and largely no significant differences. They lost weight at a mean rate of < 40 µg/sec.

The combined ranking based on burning characteristics (Table 3) indicates how well the needles of these 13 species will contribute to fire. The top seven species are separated by only 9 points, whereas the bottom six species are separated by 37 points. Ponderosa pine and Jeffrey pine are separated by one point. These two species ranked in the upper half of every burning characteristic except flame time. Monterey pine, coast redwood, and knobcone pine are separated by merely four points. Giant sequoia and sugar pine are separated by two points. All of these species contribute well to fire. With a few exceptions, they were in the upper half of the burning characteristics (Table 2). The species at the bottom of Table 3 (Douglas-fir, Pacific silver fir, subalpine fir, and western hemlock) were the bottom four species in every category except flame time. These four species contribute poorly to fire.

TABLE 3. Combined ranking of species based on six burning characteristics.

RANK	SPECIES	POINTS
1	Ponderosa pine	24
2	Jeffrey pine	25
3	Monterey pine	27
4	Coast redwood	29
5	Knobcone pine	31
6	Giant sequoia	32
7	Sugar pine	33
8	Lodgepole pine	37
9	Western redcedar	45
10	Douglas-fir	59
11	Pacific silver fir	63
12	Subalpine fir	67
13	Western hemlock	74

Discussion

The burning characteristics tested in this study address important aspects of nonwoody fuel flammability in coniferous forests. Flame height, flame time, ember time, and burn time measure the intensity and duration of a burnable condition in the needles, so that a spreading fire can be supported. Percent combusted and mean weight loss rate indicate how much of the fuel bed will be involved with fire and how quickly the fuel will be consumed. No single characteristic defines flammability, especially on the community level, when only nonwoody fuels are considered. Taken together, however, the characteristics in Table 2 speak to the role of fire in the forests in which these 13 species are dominant. The top ranked species in these categories are prominent in forests in which fire is common. Some of these forests are fire-stable, others are fire-resilient with FRI on the order of a few decades.

Ponderosa pine and Jeffrey pine, the top two ranked species (Table 3) grow in forests with short FRI. Studies of fire history in ponderosa pine at various locations in the Rocky Mountains and the Sierra Nevada and Cascade Ranges put the FRI at less than 15 yr (Arno 1980; Madany and West 1980; Arno and Peterson 1983; Swetnam and Dieterich 1983; van Wagtendonk 1983; Agee 1994). Fires may be even more frequent in Jeffrey pine forests (Vogl 1967), and they clearly favor Jeffrey pine (Sweeney 1967; Vogl 1967). Both species are resisters (Table 1). They exist in fire-stable forests, where frequent underburns are supported largely by nonwoody fuels. The burning characteristics indicate that surface fires would be well-supported, and the fuels would be consumed rapidly and almost completely (Table 2).

Monterey pine, coast redwood, and knobcone pine are prominent members of forest stands along the northern California coast into southern Oregon. Fire is a common environmental factor in this region (Vogl et al. 1977; Stuart 1987; Greenlee and Langenheim 1990; Brown and Swetnam 1994), and the forests generally are fire-resilient. Because of serotinous cones and voluminous seed crops released by fire, Monterey pine is adapted to stand-replacing fires, although surface fires also burn in these forests (Vogl et al. 1977). Knobcone pine, with 33-50 yr FRI (Vogl et al. 1977), depends on stand-replacing fires to open serotinous cones to repopulate the postfire site (Vogl 1973). Both pines are evaders (Table 1). The FRI for coast redwood is on the order of 6-8 yr (Brown and Swetnam 1994) to 135 yr (Greenlee and Langenheim 1990), and at least in the Santa Cruz Mountains some of these fires can be extensive. Fires in forests dominated by Monterey pine and knobcone pine are much more intense and more severe than fires in ponderosa pine forests, largely because of the greater woody fuel component. Fires in coast redwood forests vary from low to high severity (Greenlee and Langenheim 1990; Brown and Swetnam 1994). Fires in all three forest types are sustained because the highly flammable nonwoody fuels ignite longer time-lag woody fuels. These three species had no significant differences among them for flame height, ranking just behind ponderosa pine and Jeffrey pine (Table 2). Furthermore, they ranked in the top five for burn time.

Giant sequoia, the number six species, grows in a series of isolated groves in the Sierra Nevada Range, for which historic FRI ranged from 5-8 yr from 500 to 800 AD and from 2-4 yr from 1000 to 1300 AD (Swetnam 1993). Similar to ponderosa pine and Jeffrey pine, the forests were fire-stable and the fires were low intensity, low severity surface burns (Kilgore 1972; Bonnicksen and Stone 1982). Giant sequoia is a resister (Table 1). Giant sequoia had a long burn time and ~76% fuel consumed (Table 2), which, coupled with the short FRI, indicates that most of the fuel consumed by natural fires was nonwoody.

The relationship between sugar pine and fire is known from studies of mixed conifer forests in the Sierra Nevada and Cascades (Kilgore 1972; van Wagtendonk 1983; Thomas and Agee 1986). Sugar pine is a prominent subordinate species in giant sequoia and ponderosa pine forests. Mature sugar pines resist fire (Table 1). Sugar pine's presence in the community depends on frequent fires removing its main competitor, white fir. The model created by van Wagtendonk (1983) showed that sugar pine seedlings were favored by an open landscape, presumably created by fire. Sugar pine density remained above 600 trees/ha through 80 yr of lightning fires at mean intervals of 8.9 yr. Sugar pine may be more susceptible to postfire insect attack than to the fire itself (Thomas and Agee 1986). Although sugar pine ranks just below giant sequoia, and considerably below ponderosa pine (Table 3), the contribution of sugar pine needles to regular fires in these forests is important. It is noteworthy that 77% of sugar pine fuel was consumed at a rate of 50.9 µg/sec, and that it had a long flame time (Table 2). Mixed with either giant sequoia or ponderosa pine needles, sugar pine enhances the flammability of the fuel load.

The bottom six species in Table 3 exist in dramatically different fire regimes from the top seven species. Fires in communities dominated by these species usually are high intensity, high severity, and stand-replacing. Lodgepole pine, Douglas-fir, and subalpine fir are associated with fire-resilient forests in the Pacific Northwest, and owe their continued dominance on the landscape to stand-replacing fires at FRI on the order of 150-200 yr or more (Fonda and Bliss 1969; Fonda 1976; Arno 1980; Agee and Smith 1984; Romme and Knight 1981; Romme and Despain 1989; Taylor and Fonda 1990; Agee 1993). All three species are postfire invaders (Agee 1993), and depend on abundant seed crops to restore the forest community. Some lodgepole pine and Douglas-fir forests, however, are known to support surface burns on shorter intervals (Morrison and Swanson 1990; Agee 1991, 1994; Wetzel 1995). Lodgepole pine had the highest rank among these six species (Table 3), four points lower than sugar pine. Lodgepole pine needles, however, will not sustain fire in young forests for which there is little woody fuel (Romme and Despain 1989). Forests dominated by lodgepole pine, Douglas-fir, and subalpine fir rely on decades of accumulated woody fuels to support fires, rather than the less flammable needles investigated in this study.

Western redcedar, Pacific silver fir, and western hemlock are avoiders (Table 1), favored by the absence of fire (Fonda and Bliss 1969; Hemstrom and Franklin 1982; Agee et al. 1990; Agee 1993, 1994). These species are common in Pacific Northwest forests. The data in Table 2 confirm that the nonwoody fuels of these three species contribute little to the fire environment of their communities. Of the three, western redcedar contributed best to sustainability, however, they all ranked near the bottom on measures of intensity and consumability.

Acknowledgements

It is a pleasure to acknowledge Lisa Myers and Jeff Manlay of Sequoia National Park, and Carol Trent, for their help with the needle collections. Thanks to Jan van Wagtendonk and a reviewer, who contributed valuable suggestions on the focus of the manuscript.

Literature Cited

Agee, J. K. 1989. Wildfire in the Pacific west: a brief history and implications for the future. *In* N. H. Berg (Tech. Coord.) Proc. Symp. Fire and Watershed Management. USDA For. Serv. Gen. Tech. Rep. PSW-109. Pacific Southw. For. Range Exp. Sta., Berkeley, Calif. Pp. 11-16.

_____. 1991. Fire history of Douglas-fir forests in the Pacific Northwest. *In* L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff (tech. coords.) Wildlife and vegetation of unmanaged Douglas-fir forests. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-285. Pacific Northw. Res. Sta., Portland, Oregon. Pp. 25-33.

_____. 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Covelo, California.

_____. 1994. Fire and weather disturbances in terrestrial ecosystems of the eastern Cascades. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-320. Pacific Northw. Res. Sta., Portland, Oregon. 52 p.

Agee, J. K., M. Finney, and R. de Gouvenain. 1990. Forest fire history of Desolation Peak, Washington. Can. J. For. Res. 20: 350-356.

Agee, J. K., and L. Smith. 1984. Subalpine tree reestablishment after fire in the Olympic Mountains, Washington. Ecology 65: 810-819.

Arno, S. F. 1980. Forest fire history in the northern Rockies. J. For. 78: 460-465.

Arno, S. F., and T. D. Peterson. 1983. Variation in estimates of fire intervals: a closer look at fire history on the Bitterroot National Forest. USDA For. Serv. Res. Paper INT-301. Intermountain For. Range Exp. Sta., Odgen, Utah. 8 p.

Bond, W. A., and J. J. Midgley. 1995. Kill thy neighbour: an individualistic argument for the evolution of flammability. Oikos 73: 79-85.

Bonnicksen, T. M., and E. C. Stone. 1982. Reconstruction of a presettlement giant sequoia-mixed conifer forest community using the aggregation approach. Ecology 63: 1134-1148.

Brown, P. M., and T. W. Swetnam. 1994. A cross-dated fire history from coast redwood near Redwood National Park, California. Can. J. For. Res. 24: 21-31.

Finney, M. A., and R. E. Martin. 1989. Fire history in a *Sequoia sempervirens* forest at Salt Point State Park, California. Can. J. For. Res. 19: 1451-1457.

Fonda, R. W. 1976. Fire-resilient forests of Douglas-fir in Olympic National Park: an hypothesis. *In* R. M. Linn (ed.) Proc. First Conf. Sci. Research Natl. Parks. USDI Natl. Park Serv. Trans. Proc. Series, No. 5. Supt. Doc., Washington, D. C. Pp. 1239-1242.

Fonda, R. W., and L. C. Bliss. 1969. Forest vegetation of the montane and subalpine zones, Olympic Mountains, Washington. Ecol. Monogr. 39: 271-301.

Greenlee, J. M., and J. H. Langenheim. 1990. Historic fire regimes and their relation to vegetation patterns in the Monterey Bay area of California. Amer. Midl. Nat. 124: 239-253.

Habeck, J. R., and R. W. Mutch. 1973. Fire-dependent forests in the northern Rocky Mountains. Quaternary Res. 3: 408-424.

Hemstrom, M. A., and J. F. Franklin. 1982. Fire and other disturbances of the forests in Mount Rainier National Park. Quaternary Res. 18: 32-51.

Hickman, J. C. (ed.) 1993. The Jepson Manual: Higher Plants of California. University of California Press, Berkeley, California.

Holling, C. S. 1973. Resilience and stability of ecological systems. Ann. Rev. Ecology and Systematics 4: 1-23.

Keeley, J. E. 1977. Fire-dependent reproductive strategies in *Arctostaphylos* and *Ceanothus*. *In* H. A. Mooney and E. C. Conrad (tech. coords.) Proc. Symp. Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems. USDA For. Serv. Gen. Tech. Rep. WO-3. Supt. Doc., Washington, D. C. Pp. 391-396.

Kilgore, B. M. 1972. Impact of prescribed burning on a sequoia-mixed conifer forest. Proc. Tall Timbers Fire Ecol. Conf. 12: 345-375.

Kilgore, B. M., and D. Taylor. 1979. Fire history of a sequoia-mixed conifer forest. Ecology 60: 129-142.

Komarek, E. V. 1968. Lightning and lightning fires as ecological forces. Proc. Tall Timber Fire Ecol. Conf. 8: 169-197.

Madany, M. H., and N. E. West. 1980. Fire history of two montane forest areas of Zion National Park. *In* M. A. Stokes and J. H. Dieterich (tech. coords.) Proc. Fire History Workshop. USDA For. Serv. Gen. Tech. Rep. RM-81. Rocky Mtn. For. Range Exp. Sta., Fort Collins, Colorado. Pp. 50-56.

Martin, R. E., D. A. Gordon, M. E. Gutierrez, D. S. Lee, D. M. Molina, R. A. Schroeder, D. B. Sapsis, S. L. Stephens, and M. Chambers. 1994. Assessing the flammability of domestic and wildland vegetation. *In* Proc. 12th Internatl. Conf. Fire and Forest Meteorology. Soc. Amer. For., Bethesda, Maryland. Pp. 130-137.

Morrison, P. H., and F. J. Swanson. 1990. Fire history and pattern in a Cascade Range landscape. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-254. Pacific Northw. Res. Sta., Portland, Oregon. 77 p.

Mutch, R. W. 1970. Wildland fires and ecosystems - an hypothesis. Ecology 51: 1046-1051.

Odum, E. P. 1969. The strategy of ecosystem development. Science 164: 262-270.

Pyne, S. J., P. L. Andrews, and R. D. Laven. 1996. Introduction to Wildland Fire (2nd ed.). John Wiley & Sons, New York.

Romme, W. H., and D. G. Despain. 1989. Historical perspective on the Yellowstone fires of 1988. BioScience 39: 695-699.

Romme, W. H., and D. H. Knight. 1981. Fire frequency and subalpine forest succession along a topographic gradient in Wyoming. Ecology 62: 319-326.

Stuart, J. D. 1987. Fire history of an old-growth forest of *Sequoia sempervirens* (Taxodiaceae) forest in Humboldt Redwoods State Park, California. Madrono 34: 128-141.

Sweeney, J. R. 1967. Ecology of some fire type vegetation in northern California. Proc. Tall Timbers Fire Ecol. Conf. 7: 111-125.

Swetnam, T. W. 1993. Fire history and climate change in giant sequoia groves. Science 262: 885-889.

Swetnam, T. W., and J. H. Dieterich. 1983. Fire history of ponderosa pine forests in the Gila Wilderness, New Mexico. *In* J. E. Lotan, B. M. Kilgore, W. C. Fischer, and R. W. Mutch (tech. coords.) Proc. Symp. Workshop Wilderness Fire. USDA For. Serv. Gen. Tech. Rep. INT-182. Intermtn. For. Range Exp. Sta., Ogden, Utah. Pp. 390-397.

Taylor, K. L., and R. W. Fonda. 1990. Woody fuel structure and fire in subalpine fir forests, Olympic National Park, Washington. Can. J. For. Res. 20: 193-199.

Thomas, T. L., and J. K. Agee. 1986. Prescribed fire effects on mixed conifer forest structure at Crater Lake, Oregon. Can. J. For. Res. 16: 1082-1087.

van Wagtendonk, J. W. 1983. Fire suppression effects on fuels and succession in short-fire-interval wilderness ecosystems. *In* J. E. Lotan, B. M. Kilgore, W. C. Fischer, and R. W. Mutch (tech. coords.) Proc. Symp. Workshop Wilderness Fire. USDA For. Serv. Gen. Tech. Rep. INT-182. Intermtn. For. Range Exp. Sta., Ogden, Utah. Pp. 119-129.

Vogl, R. J. 1967. Fire adaptations of some southern California plants. Proc. Tall Timbers Fire Ecol. Conf. 7: 79-109.

_____. 1973. Ecology of knobcone pine in the Santa Ana Mountains, California. Ecol. Monogr. 43: 125-143.

Vogl, R. J., W. P. Armstrong, K. L. White, and K. L. Cole. 1977. The closed-cone pines and cypresses. *In* M. Barbour and J. Major (eds.) Terrestrial Vegetation of California. John Wiley and Sons, New York. Pp. 295-358.

Received 16 May 1997
Accepted for publication 16 December 1997

Weaver, H. 1967. Fire as a continuing ecological factor in perpetuation of ponderosa pine forests in western United States. Adv. Front. Plant Sci. 18: 137-154.

Westman, W. E., and J. F. O'Leary. 1986. Measures of resilience: the response of coastal sage scrub to fire. Vegetatio 65: 179-189.

Wetzel, S. A. 1995. Fire history of *Pseudotsuga menziesii* forests of the Morse Creek drainage of Olympic National Park, Washington. Western Washington University, Bellingham. M.S. Thesis.

Zar, J. H. 1996. Biostatistical Analysis (3rd ed.). Prentice-Hall, Inc. Upper Saddle River, New Jersey.

Andrea Woodward,[1] Field Station for Protected Area Research, College of Forest Resources, University of Washington, Box 352100, Seattle, Washington 98195-2100

Relationships Among Environmental Variables and Distribution of Tree Species at High Elevation in the Olympic Mountains

Abstract

Relationships among environmental variables and occurrence of tree species were investigated at Hurricane Ridge in Olympic National Park, Washington, USA. A transect consisting of three plots was established down one north- and one south-facing slope in stands representing the typical elevational sequence of tree species. Tree species included subalpine fir (*Abies lasiocarpa*), Douglas-fir (*Pseudotsuga menziesii*), mountain hemlock (*Tsuga mertensiana*), and Pacific silver fir (*Abies amabilis*). Air and soil temperature, precipitation, and soil moisture were measured during three growing seasons. Snowmelt patterns, soil carbon and moisture release curves were also determined. The plots represented a wide range in soil water potential, a major determinant of tree species distribution (range of minimum values = -1.1 to -8.0 MPa for Pacific silver fir and Douglas-fir plots, respectively). Precipitation intercepted at plots depended on topographic location, storm direction and storm type. Differences in soil moisture among plots was related to soil properties, while annual differences at each plot were most often related to early season precipitation. Changes in climate due to a doubling of atmospheric CO_2 will likely shift tree species distributions within, but not among aspects. Change will be buffered by innate tolerance of adult trees and the inertia of soil properties.

Introduction

Mountainous areas have steep gradients of moisture and temperature (Whittaker, 1975), and provide the opportunity to study biologically significant differences in environment over short distances. These gradients are caused by orographically induced precipitation patterns, adiabatically and topographically induced changes in temperature, and hydrologic processes that redistribute water in steep terrain (Barry, 1992; Ambroise, 1995). The resulting vegetation pattern is typified by closely spaced ecotones, and because of the overwhelming influence of environmental factors, may be especially sensitive to climate change.

Landscape-level effects of global climate change (GCC) on vegetation will manifest at the scale of species distributions of physiognomically dominant organisms. Describing environmental conditions controlling patterns at this scale is one approach to understanding effects of predicted changes in temperature and precipitation due to GCC. In addition to determining the magnitude of environmental difference driving vegetation pattern, relationships among variables predicted by general circulation models (e.g., temperature and precipitation) and other driving variables (e.g., soil moisture) can be evaluated.

This study describes environmental conditions that are associated with the occurrence of dominant tree species in the northeastern Olympic Mountains, Washington. The study was conducted in stands including subalpine fir (*Abies lasiocarpa*), mountain hemlock (*Tsuga mertensiana*), Pacific silver fir (*Abies amabilis*), and Douglas-fir (*Pseudotsuga mensiezii*). These stands were closely spaced, but they include species that are diagnostic of vegetation zones (sensu Henderson et al. 1989) which define vegetation pattern at a much larger scale. Critical variables affecting subalpine vegetation in temperate climates include snowmelt, length of growing season, soil and air temperatures, and midsummer soil drying (Tanquillini, 1979; Stevens and Fox, 1991). Measurements of these variables were conducted regularly during three growing seasons and complement studies of environmental-species relationships using less frequent measurements over a wider geographic area (e.g., Zobel et al., 1976; Henderson et al., 1989).

Site Description

Study plots were established on Hurricane Ridge (1550 m, 123° 30' N lat., 47° 58' E long.) near the northern border of Olympic National Park (Figure

[1]Current address: USGS-Biological Resources Division, Forest and Rangeland Ecosystem Science Center, Olympic Field Station, 600 E. Park Avenue, Port Angeles, WA 98362

© 1998 by the Northwest Scientific Association. All rights reserved.

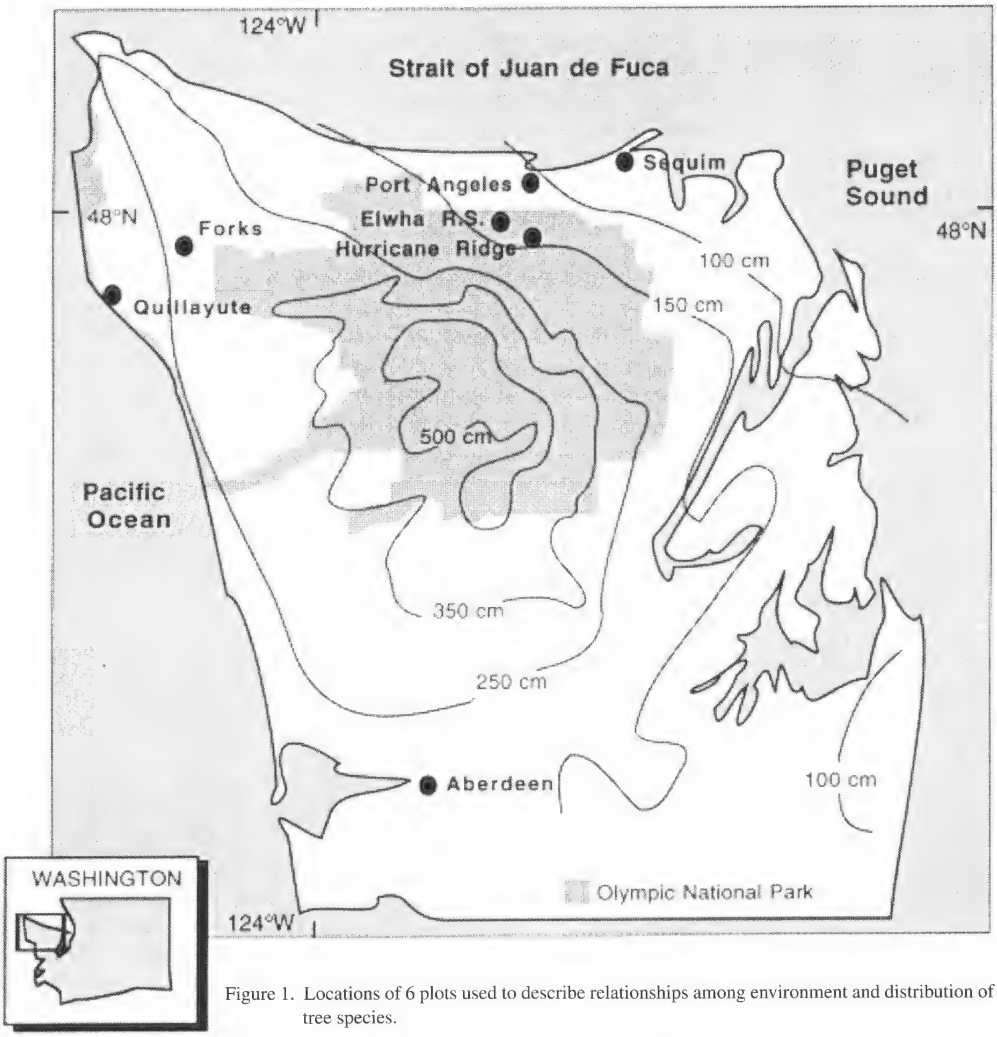


Figure 1. Locations of 6 plots used to describe relationships among environment and distribution of tree species.

1). The Ridge is oriented east-west and is at or below treeline for most of its length. It is composed of Eocene basalts and slightly younger marine sediments including sandstones, shales, and conglomerates (Tabor, 1987). Soils are classified as Typic Cryumbrepts. Subalpine fir (*Abies lasiocarpa*) is the most abundant species on north and south aspects near the ridgeline. Mountain hemlock (*Tsuga mertensiana*) occurs with subalpine fir down north-facing slopes, grades into stands of Pacific silver fir (*Abies amabilis*)and eventually into stands of Douglas-fir (*Pseudotsuga mensiezii*) and western hemlock (*Tsuga heterophylla*) at the base of the mountains. Subalpine fir grades into Douglas-fir at lower elevations on south-facing slopes (Henderson et al., 1989).

The Olympic Peninsula experiences a maritime climate. Most storms move across the peninsula from the southwest (Speer, 1986) and deposit over 600 cm of average annual precipitation on Mount Olympus (2430 m; Philips and Donaldson, 1972). The northeast Olympics are in a rainshadow and Hurricane Ridge averages approximately 100-150 cm precipitation annually, of which 80% falls during October-March and 5% falls July-August. Average January temperatures below 1000 m in the

northeast Olympic Peninsula are ~0 °C; maximum August temperatures are ~21 °C (National Oceanic and Atmospheric Administration, 1978).

Two transects each consisting of three 20 x 20 m plots were established. One was on a north- and one was on a south-facing slope. Each transect described a gradient of tree dominance (Table 1). The top of the north transect (ALN) was at 1523 m in a stand of subalpine fir, and extended for 70 m of elevation going through a mixed stand of subalpine fir and mountain hemlock (ALTM), and ending in a Pacific silver fir stand with mountain hemlock in the understory (AA). The south transect spanned 116 m in elevation, starting in a subalpine fir stand (ALS), going through a mixed stand of subalpine fir and Douglas-fir (ALPM), and ending in a Douglas-fir stand (PM).

Methods

Air and soil temperatures, precipitation, soil moisture, and snowmelt were used to characterize growing season conditions during the study. Soil carbon, soil moisture release curves and potential incident solar radiation were used to describe relatively invariant features of the plots.

Temperatures

Air temperature was recorded weekly using max-min thermometers mounted at 1 m height in partial shade on stakes near the center of each plot. Measurements were made from 30 June until 27 November 1993, 10 April to 21 October 1994, and 13 May to 12 October 1995. Records for individual plots commenced when stakes were free of snow in 1994 and 1995. In addition, single-sensor data loggers (Model Hobo-Temp, Onset Computer Co., Inc., Pocasset MA) were installed on 27 November 1993 and recorded air temperature 5 times daily until 11 November 1994. The dataloggers were covered with plastic, put in small plastic containers having holes for ventilation, and hung in trees at approximately 2 m height. Monthly average air temperatures calculated from dataloggers and max-min thermometers when both

TABLE 1. Plot characteristics along north and south facing transects on Hurricane Ridge, Olympic Mountains. Plots are 20 x 20 m and are numbered from top to bottom of transects.

	Plot					
	ALN	ALTM	AA	ALS	ALPM	PM
Location						
Elevation(m)	1523	1503	1453	1520	1463	1404
Aspect (°)	35	38	35	213	190	228
Slope (°)	17	9	32	9	14	22
Plant Community						
Tree area/plot[1] (m^2)						
Abla	3.49	2.90	–	3.21	1.52	0.41
Tsme	0.07	0.33	0.24	–	–	–
Abam	–	–	3.84	–	–	–
Psme	–	–	–	0.09	0.94	2.19
Total	3.56	3.23	4.08	3.30	2.46	2.60
Understory[2] (trees < 2m tall)						
	Abla	Abam (Tsme) (Abam)	Abam (Tsme) (Abla)	Abla	Abla	(Abla)
Soils						
Texture[3]	L-SL	L-SL	SSiL	SL	SGL	SGL
Moisture at:						
Field Capacity (%)	40.3	41.4	43.6	37.8	33.4	27.3
Permanent Wilt (%)	16.3	17.4	20.6	15.5	14.0	8.2
Carbon (%)	5.6	6.4	8.5	7.0	4.0	3.6

[1]Area at breast height based on dbh measurements; abbreviations are for subalpine fir (Abla), mountain hemlock (Tsme), Pacific silver fir (Abam) and Douglas-fir (Psme).

[2]Species in parentheses had <5% cover; others had 6-25% cover.

[3]Loam (L), sandy (S), silt (Si), gravelly (G).

were available rarely differed more than 1 °C with max-min thermometers tending to give the higher values.

Soil temperatures were recorded from buried copper-constantan or chromel-alumel thermocouples using a hand-held electronic thermometer. Thermocouples were buried in pairs at 6 cm and 35 cm below the soil surface, with 4 pairs per plot. Pairs were located randomly in each quadrant of the plot by throwing an object over the shoulder. Readings were made at mid-day, bi-weekly from 27 July to 3 November 1993 and 10 April 1994 to 20 May 1994, and weekly from 3 June to 21 October 1994 and 8 June to 12 October 1995.

Precipitation

Throughfall precipitation was measured weekly using cylindrical, funnel-topped rain gauges mounted on the same stakes as the max-min thermometers from 30 June to 3 November 1993, 10 April to 21 October 1994, and 25 May to 12 October 1995. The gauges were partially under canopy, but not under canopy driplines. It was impossible to locate rain-gauges on the ground away from the influence of trees in these plots.

Long-term average of maximum snow depth was estimated from height of lichens growing on tree trunks (Long, 1982). The plots were visited bi-weekly beginning 10 April 1994 and weekly beginning 13 May 1995 to estimate when plots were completely bare of snow.

Soil Moisture

Soil moisture was estimated bi-weekly from four samples taken at 15 cm depth and randomly located in each quadrant of the plot by throwing an object over the shoulder. Samples were collected into heavy plastic bags, labeled and taken to the lab. Two approximately 10 g subsamples were taken from each bag and gravel >2-4 mm in diameter was removed as quickly as possible. These samples were weighed, dried at least 12 hrs at 105 °C, and reweighed to determine gravimetric water content. Some samples (n = 48) were also dried for 24 hours and demonstrated that no significant additional drying occurs between 12 and 24 hours.

Soil moisture release curves were developed so soil moisture percentages could be expressed as soil water potential (Richards, 1949). Composites of 6 samples from each site were subsampled and gravel > 2-4 mm was removed so they were similar to samples used for soil moisture determinations. Two sets of 4 subsamples were used to represent each site. One set was used to determine moisture content at pressure values of .033, 0.1, 0.3, and 0.5 MPa. The other set was used for 0.1, 0.2, 0.5 and 1.5 MPa. Two sets were used because the samples no longer produced results describing a smooth curve after several cycles of wetting and drying. The two sets gave consistent values for 0.1 and 0.5 MPa of pressure.

Soil Carbon

Subsamples of the composite soil samples used for moisture release curves were sieved to < 2 mm and finely ground with a mortar and pestle for each site. They were analyzed for carbon content using a total CHN analyzer (Perkin-Elmer CHN Analyzer Model 2400; Page et al. 1982).

Potential Incident Solar Radiation

Plot locations were determined using a portable global positioning system (GPS) and entered into a geographic information system (GIS). Values for potential incident solar radiation (PISR) were calculated for the entire 22nd day of each month using the Solarflux model (Hetrick et al. 1993) for each plot. The model uses solar angle, slope, aspect and local topographic shading derived from USGS 7.5 minute digital elevation models with 30 x 30 m resolution to approximate radiation for a given point. The model does not account for shading due to vegetation or cloud cover.

Weather Data

Individual storms were described using daily weather maps (National Oceanic and Atmospheric Administration, 1993-1995b), and radiosonde soundings taken on the coast at Quillayute (National Climatic Data Center 1993-1995; Figure 1). The 700 millibar (mb) sounding used here corresponds to approximately 3050 m elevation, or slightly higher than the highest point in the Olympic Mountains.

Stand Age

Two cores were taken in November 1995 at 1.4 m height from 8 trees of each dominant or co-dominant species at plots ALTM, AA, ALPM, and PM as part of another study. Tree age was

determined by counting annual rings of cores and adding 10 years to compensate for core height. If the core did not include the pith, missing rings where estimated based on extrapolating pith location from the curvature of rings included in the core. Not all cores could be aged.

Statistical Methods

Summary statistics for environmental variables were calculated for each plot. Weekly air and soil temperatures from each plot were averaged across the maximum number of available weeks during the growing season (weeks 26-40), and expressed as heat sums (degree-days) above 0 °C from snowmelt in the spring to snowfall in the fall for 1994. Precipitation was summed for the entire growing season (weeks 26-40) and the early growing season (weeks 26-31). Soil moisture was summarized as a cumulative water potential value (MPa-days).

Precipitation measured at the plots was compared for storms > 25 mm at ALN. Storms were categorized based on average wind direction measured by the Quillayute radiosonde at 700 mb: south to southwesterly (compass degrees 175-217), westerly (compass degrees 250-262), and northwesterly (compass degrees 286-334). Storms were also classified by type based on daily weather maps (National Oceanographic and Atmospheic Administration 1993-1995b) Precipitation coinciding with passage of a front was considered a frontal storm; precipitation occurring in association with a stationary or slowly moving low, in the absence of a front, was considered a convective storm (Philips and Donaldson 1972). Differences in precipitation at plots due to storm type were evaluated using a general linear models procedure (SAS Institute, 1988). Least-squares means were used to compensate for unequal group sizes. Spearman rank correlations were used to compare precipitation distribution among plots due to storm type. Ranks were used to reduce variance due to storm size.

Stepwise regression (SAS Institute 1988) was used to describe the relative importance of variables determining soil moisture. Data from all plots were combined to evaluate the importance of average maximum and minimum air temperatures and heatsums, average soil temperature, total growing season precipitation, early (weeks 26-31) and late (weeks 32-40) growing season precipitation, PISR, soil carbon, snowmelt timing, field capacity, permanent wilting point, aspect, and slope. Regressions were also run by plot to evaluate listed variables that vary annually (air and soil temperatures and precipitation). Because of the small number of years (n = 3) variables significant at $p < 0.15$ were reported for plots.

Results

Air Temperatures

As expected, results from data loggers show that average air temperature was generally higher on the south transect than the north (Figure 2). South transect plots had fewer months with average temperature below 0 °C in the winter. Plot ALS was the coolest plot on the south transect; plot AA was the coolest northern plot from April through October, but the warmest during November through February.

The less extreme climate at AA compared with ALN and ALTM was also shown by the averages of maximum and minimum air temperatures during weeks 26-40 (Table 2). Plot AA had the lowest maximum temperatures on the north transect (difference from ALN and ALTM = 0.5-3.0 °C), but had the highest minimum air temperatures (difference from ALN and ALTM = 0.3-1.0 °C).

Growing season length varied with site. Based on number of weeks with freezing temperatures in 1993 and frost-free periods in 1994 and 1995 (Table 2), plots PM, ALPM, and AA had the longest growing seasons, plot ALN the shortest, and ALTM and ALS were intermediate. Higher heatsums from snowmelt to snowfall (PM, ALPM, AA) were associated with earlier snowmelt (Table 2).

Soil Temperatures

Early season soil temperature records are available for 1994 and 1995 and show soils warmed first at ALPM and PM, and last at ALN and ALTM (Figure 3 shows ALN and PM), reflecting order of snowmelt (Table 2). Snow melted at AA at the same time as at ALPM but colder air temperatures on the north transect prevented soil temperatures from warming as quickly as ALPM during both years.

Following snowmelt, average soil temperatures (average of 6 and 30 cm; Figure 3) generally

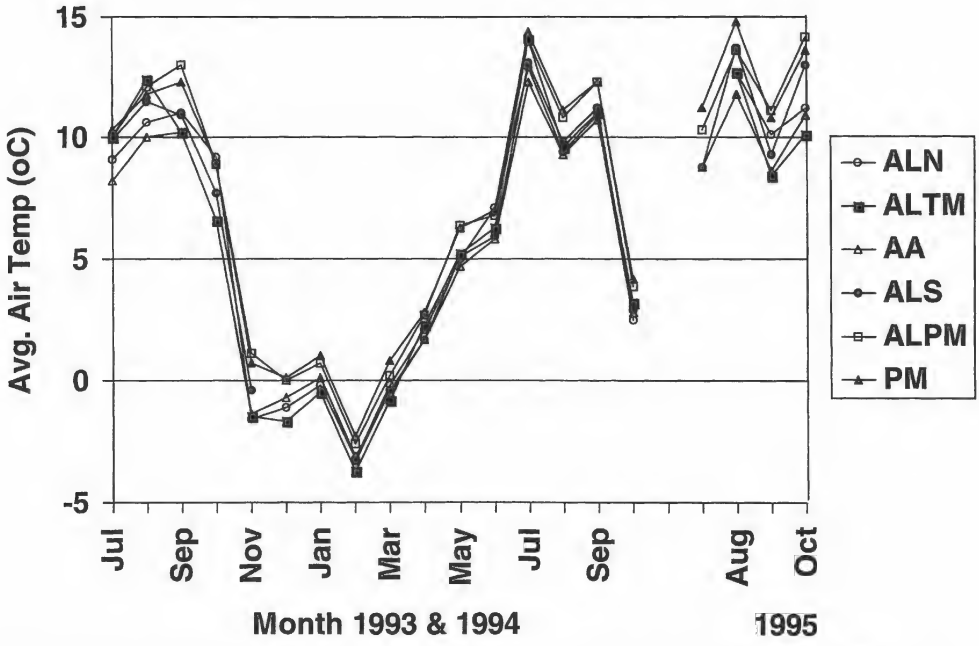


Figure 2. Monthly average of maximum and minimum air temperature at 6 plots from July 1993 to October 1994 and June to September 1995. Data from November 1993 to October 1994 are from dataloggers; others are from max-min thermometers.

followed patterns of average air temperature (Figure 2): peaks of both occurred in September 1993 (weeks 36-39), and July (weeks 27-30) and September (weeks 36-39) of 1994 and 1995. However, soil at 35 cm depth heated more slowly in the spring and cooled more slowly in the fall than soil at 6 cm. South-facing plots had higher average soil temperatures during the growing season (especially ALPM and PM) than the north, reflecting corresponding differences in air temperature and insolation (Table 2).

Soil temperature showed consistent patterns among plots when weekly plot means were compared using least significant difference tests. Plots ALPM and PM were significantly warmer than all other plots in 40 of the 44 weeks for which comparisons could be made. In 35 weeks, at least two other groups were distinguished. Plots AA and ALS usually fell in the intermediate group (counts in intermediate group = 63%, AA; 80%, ALS), and plots ALN and ALTM usually had the coldest soils (counts in lowest group = 54% ALN; 80%, ALTM).

Precipitation

Total precipitation during the growing season (July-September, weeks 27-39) was 81% of average at Elwha in 1993, 60% of average during 1994, and 136% of average in 1995 (National Oceanic and Atmospheric Administration, 1993-1995a, based on 30 yr average). The patterns of precipitation also differed among years 1993, 1994, and 1995, and from the pattern averaged over 20 years by week (Figure 4). The average pattern at Elwha shows that the driest summer period normally occurs at the end of July and early August (weeks 30-33). The precipitation record from ALN (Figure 4) shows drought later than normal in 1993 (weeks 35-39), three dry periods in 1994 (weeks 28-31, 33-35, 38-40) and two short dry periods in 1995 (weeks 26-27, 37-38).

Amount of precipitation at plots did not vary significantly ($p < 0.05$) with storm direction, possibly due to the small number of observations and large variability among storms for size. However, distribution of precipitation among plots

TABLE 2. Environmental data for the 1993, 1994, and 1995 growing seasons.

	Plot					
	ALN	ALTM	AA	ALS	ALPM	PM
Air Temperature[1]						
Max. Temp. - Avg. (°C) and Heatsum (°C-days)						
1993(wks 26-40)	17.7	18.3	15.7	18.6	19.7	18.8
1994(wks 26-40)	17.6	19.3	16.3	18.5	20.3	19.3
1995(wks 26-40)	17.3	16.8	16.3	18.4	19.9	20.4
1994(melt-fall)[2]	1450	1687	1586	1656	2002	2191
Min. Temp. - Avg. (°C) and Heatsum (°C-days)						
1993(wks 26-40)	2.5	2.7	3.2	2.9	3.4	3.9
1994(wks 26-40)	3.6	4.1	4.6	4.6	4.9	5.4
1995(wks 26-40)	3.6	2.9	3.9	4.4	4.9	4.8
1994(melt-fall)[2]	846	767	996	938	1022	1207
Soil Temperature Avg. (°C) and Heatsum (°C-days)						
1993(wks 30-40)	7.1	7.6	7.3	6.3	9.5	9.7
1994(wks 30-40)	7.3	5.6	7.4	7.9	9.2	9.8
1995(wks 30-40)	6.7	6.4	6.8	7.0	8.0	8.8
1994(wks 26-40)	7.3	6.1	7.4	7.8	9.4	9.6
1995(wks 26-40)	6.9	6.2	6.9	7.2	8.3	9.1
1994(melt-fall)[2]	817	786	935	902	1179	1369
Precipitation (mm)						
1993(wks 26-40)	169	91	84	54	61	100
1994(wks 26-40)	148	99	58	54	65	49
1995(wks 26-40)	385	225	134	117	172	104
1993(wks 26-31)	109	50	58	32	41	74
1994(wks 26-31)	23	15	10	8	8	6
1995(wks 26-31)	83	40	30	29	29	20
Soil Moisture						
Water Potential Sum (MPa-days)						
1993(wks 26-40)	-11.13	-8.68	-4.20	-12.11	-16.59	-18.34
1994(wks 26-40)	-14.64	-14.63	-7.24	-21.18	-27.76	-43.96
1995(wks 25-39)	-11.41	-4.97	-5.95	-14.28	-26.60	-38.29
Snow						
Snowmelt (1994)(wk)	25	25	20	22	20	16
Snowmelt (1995)(wk)	26	27	21	22	20	<19
Max. Depth[3] (cm)	220	250	190	145	150	160
Frost-free Period						
1993						
Last Freeze (wk)	27	27	<26	26	26	26
First Freeze (wk)	41	42	42	42	43	43
Freeze during Season 31,34,	38	34,38	38,39	34,38	38	38
1994						
Last Freeze (wk)	27	25	25	25	24	24
First Freeze (wk)	40	40	41	40	41	41
1995						
Last Freeze (wk)	25	24	24	24	24	24
First Freeze (wk)	40	40	40	40	40	41
Freeze during season	—	35	—	33	—	—
Potential Incident Solar Radiation ($KJ/m^2/10^6$)						
Winter Solstice	1.2	1.2	0	1.3	1.0	1.3
Summer Solstice	40.0	40.5	40.4	39.3	42.9	41.8
Equinoxes	17.4	19.0	19.0	16.7	26.2	28.4

[1] Weeks 26-40 for both years are based on weekly readings of max-min thermometers; 1994 snowmelt to snowfall values are based on on daily records from dataloggers

[2] Snowmelt to snowfall

[3] Average of maximum snow depth based on lichen height (Long 1982)

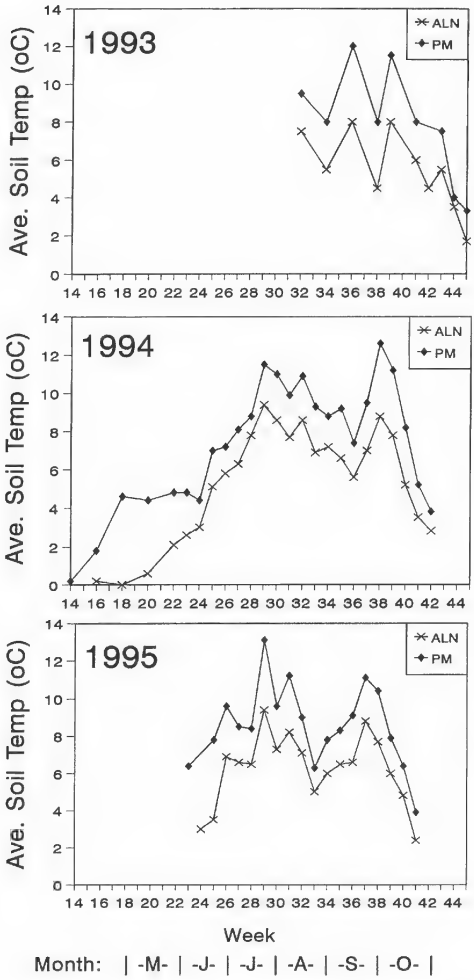


Figure 3. Weekly soil temperature averaged for depths of 6 and 35 cm during the growing seasons of 1993, 1994, and 1995 for the coldest (ALN) and warmest (PM) plots. Early season temperatures are not available for 1993.

showed three distinct patterns (Table 3): 1) all frontal storms and the one convective southwesterly storm were similar, 2) convective northwesterly, and 3) the one convective westerly storm each showed distinct patterns. Ignoring the pattern for which there was only one example, the two most frequent patterns were:

frontal W and SW: ALN > ALTM > ALPM > ALS > AA > PM

convective NW: ALN > AA > ALTM,PM > ALPM > ALS

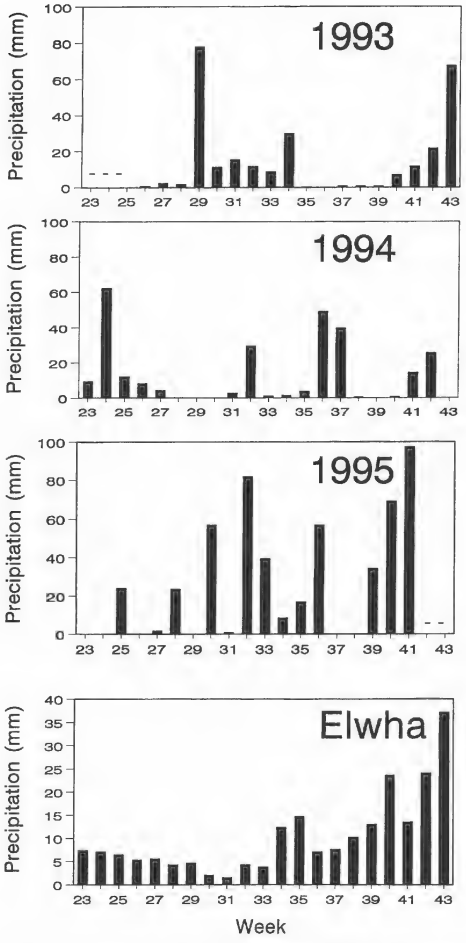


Figure 4. Weekly precipitation for plot ALN during growing seasons of 1993, 1994 and 1995, compared with 20-year average at Elwha Ranger Station.

Frontal westerly and southwesterly storms distributed precipitation on the at the top of the north and the middle of the south side of the ridge. Convective northwesterly storms distributed relatively more precipitation lower on slopes compared with the first pattern.

Soil Water Potential

Differences in soil texture and soil carbon resulted in plot specific differences in the relationship between soil moisture and soil water potential. Soil moisture at field capacity and permanent wilting increased down-slope on the north-facing

TABLE 3. Spearman rank correlations among ranks of precipitation falling at six plots due to storms categorized by direction (NW = northwesterly, W = westerly, SW = south to southwesterly) and type.

		Frontal			Convective		
		NW	W	SW	NW	W	SW
		(n=1)	(n=4)	(n=3)	(n=3)	(n=1)	(n=1)
Frontal	NW	--	0.987*	0.970*	0.329	0.647	0.986*
	W		--	0.969*	0.350	0.718	0.993*
	SW			--	0.538	0.668	0.972*
Convective	NW				--	0.462	0.343
	W					--	0.638
	SW						--

*$p < 0.02$

transect (ALN<ALTM<AA) but decreased downslope on the south-facing transect (ALS>ALPM>PM) (Table 1). These gradients corresponded to gradients of soil organic matter (estimated by soil carbon; Table 1). Plots ALN and ALS had similar values for soil moisture at field capacity and permanent wilting.

Soil water potential (Figure 5) was most variable among plots late in growing seasons when soils were relatively dry. Water potential reached -0.2 MPa at ALPM and PM by week 36 in 1993, by week 28 in 1994, and by week 23 at PM and week 29 at PM and ALPM in 1995 (Figure 5). Plot AA rarely measured below -0.1 MPa while ALTM measured as low as -3.0 MPa and ALN as low as -3.7 MPa during the study. On the south transect, ALS, ALPM, and PM had minimums of -4.1, -5.2, and -8.0 MPa, respectively. Decreases in soil water potential on the south transect sometimes lagged behind the north following storms (week 43, 1994; week 32, 1994; week 31, 1995).

Soil water potential was only partially related to annual precipitation. Most negative water potentials sums (Table 2) occurred during 1994, which had the lowest precipitation. However, most plots had more negative water potential sums in 1995 than 1993 despite higher precipitation in 1995.

Results from step-wise regression (Table 4) indicate that field capacity and minimum air temperature are the best predictors of soil moisture among plots. Annual variability of soil moisture at individual plots was predicted by early season precipitation (ALN, AA, ALS, PM), or minimum air temperature (ALPM). No variable was significant ($p < 0.15$) at ALTM.

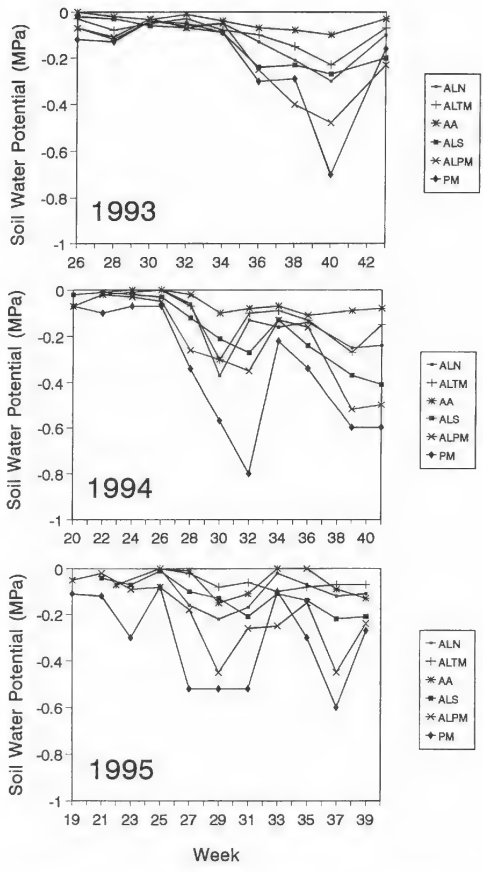


Figure 5. Soil water potential estimated from moisture release curves at 6 plots during the growing seasons of 1993, 1994 and 1995.

TABLE 4. Predictor variables for soil moisture sum. Early precipitation describes weeks 26- 31.

Site	n	Variable	Partial r^2	p
All Sites	18	Field Capacity	0.7418	0.0001
		Min. Air Temp.	0.1114	0.0042
		Soil Carbon	0.0228	0.1309
ALN	3	Early Precip.	0.9492	0.1447
ALTM	3	nothing with $p < 0.15$		
AA	3	Early Precip.	0.9999	0.0056
ALS	3	Early Precip.	0.9866	0.0740
ALPM	3	Min. Air Temp.	0.9911	0.0602
PM	3	Early Precip.	0.9997	0.0102

Potential Incident Solar Radiation

Potential incident solar radiation was highest at ALPM and PM throughout the year (Table 2). Values among plots were similar at summer solstice. Plot ALS was more similar to north transect plots than southern plots during the winter solstice and the equinoxes. Plot AA received the highest PISR among north transect plots at the equinoxes and no PISR at the winter solstice due to the low sun angle and its shaded topographic location.

Stand Ages

Dominant trees on the south transect were all of similar age. Douglas-fir at both ALPM (n = 4) and PM (n = 4) averaged 105 yr (ALPM range = 98-114; PM range = 102-110). Subalpine fir at ALPM (n = 4) averaged 103 (range = 95-110). Dominant trees on the north transect showed two age classes. Subalpine fir at ALTM was older than 150 yr (n = 3) or averaged 126 yr (n = 3, range = 124-129 yr). Mountain hemlock at ALTM were older than 150 yr (n = 2) or averaged 107 yr (n = 4, range = 94-113 yr). Most Pacific silver fir at AA were older than 150 yr (n = 5, range 154-222 yr) but one established more recently (age = 128). Although cores were not collected at ALS and ALN, neither site appeared to have the larger, older cohort, and dominant trees seemed to be similar in size to the younger cohort on ALPM and ALTM.

Discussion

Suitability of Trees as Indicators of Environment

The environmental conditions described in this study are thought to be biologically significant because they describe sites differing in dominant tree species. However, the validity of using tree species distributions to define significant contemporary gradients is questionable because tree distributions are largely determined by conditions at the time of establishment (Lassoie et al., 1985). In this study, at least one cohort of dominant trees in each stand except AA was relatively young (~100 years). The relatively uniform age of the young cohorts, the presence of charcoal in all soils, and burned branch stubs and burned snags at plot AA, suggest that the entire area experienced the same fire, though less intensely at AA. Fires were widespread in the Olympic between ca. 1870 and 1900 (Henderson et al., 1989), including the Morse Creek drainage, just east of Hurricane Ridge (Wetzel, 1995). Typically there is a 30-50 yr lag between between subalpine fires and tree reestablishment (Agee and Smith, 1984; Little and Peterson, 1994), suggesting that the study stands most likely burned in the fire of 1870. Conditions at the time of establishment were similar to the present conditions based on Washington Division 4 summary data meant to represent the central Olympic Peninsula (average annual temperature: 1895-1905 = 9.9 °C, 1985-1995 = 10.4 °C; average annual precipitation 1895-1905 = 160 cm, 1985-1995 = 154 cm). Therefore, I would expect the same species to become established in these plots if a new disturbance occurred today.

Moisture and temperature are thought to largely determine distributions of conifer species in the Pacific Northwest (Franklin and Dyrness, 1988), especially at the seed establishment and seedling stage (Lassoie et al., 1985). Douglas-fir occurred on the driest plots with highest soil and air temperatures, Pacific silver fir and mountain hemlock occurred on wet sites with intermediate temperatures, and subalpine fir occurred on the coldest sites with intermediate moisture. This distribution generally matches the relative ranks given to them for moisture optimum and tolerance to excess moisture, drought, frost and cold soils based on regional distributions (Minore 1979). This further supports the assumption that these plots describe environmental differences that distinguish among these species.

Factors Creating and Maintaining Moisture Gradients

Soil moisture, which is crucial for determining tree distribution in the Pacific Northwest, is de-

termined by the interception and redistribution of precipitation, soil moisture holding capacity, and evapotranspiration (Band et al. 1993). All of these factors are functions of temperature and precipitation, but each at different time scales and in combination with other factors. Hence it is difficult to specify the biological consequences of changes in temperature and precipitation due to GCC predicted by general circulation models.

Regional interception of precipitation is known to depend on topographic location and storm direction (Speer, 1986). This study shows that storm type and direction are also important in determining the distribution of precipitation at the local scale. Two major patterns of distribution occurred during the study. Frontal storms from the southwest, west, and northwest all produced a nearly typical orographic pattern expected of southwesterly storms (Barry, 1992; Sinclair, 1994): heaviest precipitation at the top of the leeward slope (ALN and ALTM, in this case) and large amounts on the windward slope (ALPM). This pattern would have been more typical if ALS had received more precipitation than ALPM. The second most common pattern resulted from northwesterly storms accompanied by lighter winds, and occurring during synoptic conditions conducive to convective activity (Philips and Donaldson, 1972; Pickford et al., 1980). Convective storms are caused by mountain-valley temperature gradients, and may be the main source of summer precipitation in the Olympics (Barros and Lettenmaier, 1993). Northwesterly convective storms distributed more precipitation on northerly aspects and lower on slopes than frontal storms. The dependence of rainfall pattern on storm type and direction may partially explain the weak statistical relationships seen between local topography and precipitation alone (Taylor, 1996).

Early in the growing season, and especially during and immediately after snowmelt, soil moisture can be redistributed by subsurface flow or runoff in steep topography (Band et al. 1993, Ambroise, 1995). Subsurface flow may contribute, along with other factors, to the highest level of soil moisture at AA despite receiving the least precipitation of plots on the north transect.

Soil properties are fundamentally determined by parent material, but climate plays a significant role in determining the rate and results of soil formation (Brady and Weil, 1996). In fact, differences in climate alone can explain the finer texture, higher carbon, and consequently higher water holding capacity in plot AA compared with plots ALPM and PM. Greater precipitation on the north aspects affects soil texture by causing greater transport of fine material and minerals through the soil profile by illuviation, and sediments across the landscape due to mass transport, especially by snow, compared with drier southerly sites. Higher soil carbon at plot AA compared with ALPM and PM can be explained by higher litter input due to higher site productivity (see tree areas, Table 1), limited decomposition due to cold soils, and lower quality litter due to species composition of vegetation. Specifically, litter from Pacific silver fir and mountain hemlock at plot AA decomposes more slowly than Douglas-fir litter at plots ALPM and PM (Topik, 1982). Periodic removal of litter by fire may also be less complete at plot AA if fire intensity is reduced by wetter conditions. This is supported by the observation that the 1870 fire seems to have resulted in stand replacement on the southerly plots but some trees survived on the northerly plots.

Differences in evapotranspiration among plots were not directly addressed in this study. However, the 4 °C difference between the average maximum temperature of the warmest plot (ALPM or PM) and the coldest plot (AA) each year suggests an important difference in evaporative demand. Differences in evapotranspiration, however, may be less than suggested by temperature differences alone if drought stress at dry sites results in stomatal closure.

Climate Change

General circulation models predict 2 to 4 °C increase in annual temperature in the Olympics with a doubling of CO_2 (Gates et al. 1992). The change may be the same in winter and summer, or may be higher in summer. Models also predict a 0 to 1 mm per day decrease in June-July-August precipitation (Gates et al. 1992). Predicting how changes of these magnitudes might impact the distribution of tree species depends on understanding the relative importance of factors affecting current distributions.

Differences in soil moisture among plots, represented by mean values (Figure 6), primarily reflect differences in soil properties, a relatively static feature of plots and not immediately respon-

sive to GCC. Differences among years at each plot, represented by plot ranges (Figure 6), was most often driven by early season precipitation, a variable which will be affected by GCC. Global climate change cannot be expected to alter the distribution of tree speices unless annual variability, which is driven by precipitation, results in overlap of the soil moisture conditions among plots. During 1993-1995, an average 1 mm/day variation in early season precipitation resulted in soil moisture sums at plot PM nearly including the range of values at plot ALPM, values at plot ALS nearly included the range of plot ALN, and plot ALTM included the range of plot ALN and most of plot AA (Figure 6). This range of precipitation is similar to the change predicted due to GCC and indicates that changes in soil moisture could shift the distribution of species within aspect, but not from north to south.

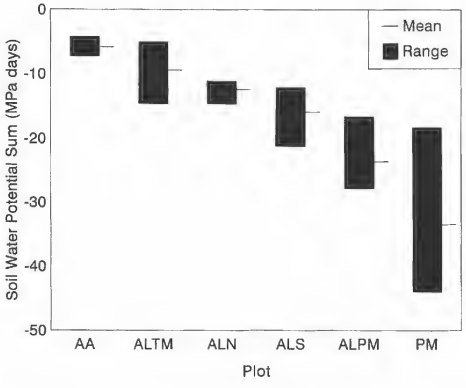


Figure 6. Soil water potential sum (Mpa-days) for 6 plots showing mean and range for three growing seasons.

Air temperature was also important in determining soil moisture differences among plots and among years at plot ALPM, as well as affecting plant physiological response. Predicted changes in temperature of 2-4 °C compare with an average maximum air temperature difference of 4 °C, and an average minimum air temperature difference of 2 °C between the coldest and warmest plots across years. Therefore, these differences can be expected to influence the distribution of tree species.

This study identifies several areas where weather models could increase our ability to predict biotic responses to GCC. First, although weather models often ignore weather patterns during the summer (Speer, 1986; Barros and Lettenmaier, 1993), conditions during the growing season have important consequences for soil moisture. Timing as well as amount of precipitation are important, as severity of summer drought appeared to be reduced by early growing season precipitation. In this study, a year with above-average precipitation (136%, 1995) distributed late in the season had similar soil moisture sums as a year with lower than average precipitation (60%, 1994) for plots ALPM and PM. An early season dry spell (1994 and 1995) may create hydrophobic soils which cannot effectively absorb rainfall later in the season (DeByle 1973), especially at the dry sites. Finally, convective and frontal storms result from different synoptic weather patterns (Lilly, 1983), and their relative frequency could alter distribution of precipitation among sites.

Changes in climate will not likely result in immediate changes in forest composition. The response of adult trees to climate is buffered by the adaptive tolerance to climate change needed by organisms surviving several centuries. In addition, climate change will not immediately impact soil properties, which have an important role in determining growing conditions. Changes may not be observed until these stands experience castrophic events, such as fire, or mortality due to old-age or disease. Instead, changes may be noticed sooner in the establishment of seedlings in subalpine meadows (Woodward et al., 1995).

Acknowledgements

I gratefully acknowledge the help of the many people who worked in the field and lab: M. Albright, M. Bivin, S. Bohlman, S. Brace, J. Burger, D. Horner, D. Peterson, S. Prichard, E. Schreiner, and N. Zolbrod. I give special thanks to L. Spier whose positive attitude was unquenchable. Weather records and maps were provided and interpreted by E. Recker and L. A. Rasmussen. B. Rochefort helped with figures. In addition, W. G. Gold, T. M. Hinckley, B. McCune, D. McKenzie, D. L. Peterson, L. A. Rasmussen, E. Rykiel Jr., E. G. Schreiner and one anonymous reviewer reviewed earlier versions of the manuscript. This research was funded by the Global Change Research Program of the National Park Service and U.S. Geological Survey, Biological Resources Division.

Literature Cited

Agee, J. K., and L. Smith. 1984. Subalpine tree establishment after fire in the Olympic Mountains, Washington. Ecology 65: 810-819.

Ambroise, B. 1995. Topography and the water cycle in a temperate middle mountain environment: the need for interdisciplinary experiments. Agric. For. Meteor. 73:217-235.

Band, L. E., P. Patterson, R. Nemani, and S. W. Running. 1993. Forest ecosystem processes at the watershed scale: incorporating hillslope hydrology. Agric. For. Meteor. 63:93-126.

Barros, A.P., and D. P. Lettenmaier. 1993. Dynamic modeling of the spatial distribution of precipitation in remote mountainous areas. Mon. Weath. Rev. 121:1195-1214.

Barry, R. G.. 1992. Mountain climatology and past and potential future climatic changes in mountain regions: a review. Mount. Res. Develop. 12:71-86.

Brady, N. C. and R. R. Weil. 1996. The Nature and Propoerties of Soils, eleventh edition. Prentice Hall, Upper Saddle River, New Jersey.

DeByle, N. V. 1973. Broadcast burning of loggin residues and the water repellency of soils. Northw. Sci. 47:77-87.

Franklin, J.F., and C. T. Dyrness. 1988. Natural Vegetation of Oregon and Washington. Oregon State University Press, Corvallis.

Gates, W. L., J. F. B. Mitchell, G. J. Boer, U. Cubash, and V. P. Meleshko. 1992. Climate modelling, climate prediction and model validation. *In* J. T. Houghton, B. A. Callander, and Varney, S. K. (eds.), Climate Change 1992: the Supplementary Report of the IPCC Scientific Assessment. University Press, Cambridge. Pp. 96-134.

Henderson, J.A., D. H. Peter,R. D. Lesher, and D. C. Shaw. 1989. Forested Plant Associations of the Olympic National Forest. USDA For. Serv. R6 Ecol. Tech. Pap. 001-88. Pacific Nortwest Region, Seattle, Washington. 502 p.

Hetrick, W.A., P. M. Rich, and S. B. Weiss. 1993. Modeling insolation on complex surfaces. *In:* Proceedings of the Thirteenth Annual ESRI User Conference, Volume 2. publisher, place. Pp. 447-458.

Lassoie, J. P., T. M. Hinckley, and C. C. Grier. 1985. Coniferous forests of the Pacific Northwest. *In* B. F. Chabot, and H. A. Mooney (eds.) Physiological Ecology of North American Plant Communities. Chapman and Hall, New York. Pp. 127-161.

Lilly, K. E. 1983. Marine Weather of Western Washington. Starpath School of Navigation, Seattle, Washington.

Little, R. L., and D. L. Peterson. 1994. Regeneration of subalpine fir (*Abies lasiocarpa*) following fire: effects of climate and other factors. Can. J. For. Res. 24:934-944.

Long, J. N. 1982. Predicting depth and duration of winter snowpack in the western Cascade mountains. Tree Plant. Notes 33:14-17.

Received 25 August 1997
Accepted 23 December 1997

Minore, D. 1979. Comparative Autecological Characteristics of Northwestern Tree Species-A Literature Review. USDA For. Serv. Gen. Tech. Rep. PNW-87. Pac. NW. Exper. Sta., Corvallis, Oregon. 72 p.

National Climatic Data Center. 1993-1995. Upper Air Rawinsonde Data. National Climate Data Center, Asheville, North Carolina.

National Oceanic and Atmospheric Administration. 1978. Climate of Washington, Climatology of the United States 60. NOAA, Washington, D.C.

_____. 1993-1995a. Climatological Data, Washington. NOAA, Washington, D. C.

_____. 1993-1995b. Daily Weather Maps. NOAA, Washington, D. C.

Page, A.L., R. H. Miller, and D. R. Keeney. 1982. Methods of Soil Analysis, Part 2: Chemical and Microbiological Properties. No. 9. American Society of Agronomy, Madison, Wisconsin.

Philips, E.L. and D. C. Donaldson. 1972. Washington Climate for these Counties: Clallam, Grays harbor, Jefferson, Pacific, and Wahkiakum. Washington State University Cooperative Extension Service. 39 p.

Pickford, S. G., G. R. Fahnestock, and R. Ottmar. 1980. Weather, fuel, and lightning fires in Olympic National Park. Northw. Sci. 54:92-105.

Richards, L. A. 1949. Methods of measuring soil moisture tension. Soil Sci. 68:95-112.

SAS Institute Inc. 1988. SAS/STAT User's Guide, Release 6.03 edition. SAS Institute Inc, Cary, North Carolina.

Sinclair, M. R. 1994. A diagnostic model for estimating orographic precipitation. J. Appl. Meteor. 33:1163-1175.

Speer, P., 1986: Precipitation analysis and modeling in western Washington. M.S. thesis, University of Washington. 163 pp.

Stevens, G. D., and J. F. Fox. 1991. The causes of treeline. Ann. Rev. Ecol. Syst. 22:177-191.

Tabor, R. W. 1987. Guide to the Geology of Olympic National Park. Pacific Northwest Parks and Forests Association, Seattle, Washington.

Taylor, W. G. 1996. Statistical relationships between topography and precipitation in a mountainous area. Northw. Sci., 70: 164-178.

Topik, C. 1982. Forest floor accumulation and decomposition in the western Cascades of Oregon. University of Oregon, Eugene. Ph.D. Dissertation.

Tranquillini, W. 1979. Physiological Ecology of the Alpine Timberline. Springer-Verlag, New York.

Wetzel, S. A. 1995. Fire history of *Pseudotsuga mensiezii* forests of the Morse Creek drainage of Olympic National Park, Washington. Washington State University, Pullman. M.S. Thesis.

Whittaker, R.H. 1975. Communities and Ecosystems, 2nd ed. MacMillan, New York.

Woodward, A., E. G. Schreiner, and D. G. Silsbee. 1995. Climate, geography, and tree establishment in subalpine meadows of the Olympic Mountains, Washington, U.S.A. Arc. Alp. Res. 27:217-225.

Zobel, D. B., A. McKee, G. M. Hawk, and C. T. Dyrness. 1976. Relationships of environment to composition, structure, and diversity of forest communities of the central western Cascades of Oregon. Ecol. Monog. 46:135-156.

Jill S. Shellenberger and **June R. P. Ross,** Department of Biology, Western Washington University, Bellingham, Washington 98225

Antibacterial Activity of Two Species of Bryozoans from Northern Puget Sound

Abstract

For the first time, bryozoan species from northern Puget Sound have been shown to contain antibacterial compounds. The antibacterial activity of two local marine cheilostome species was tested against six strains of local marine bacteria and against stock cultures of *Vibrio anguillarium*, *Bacillus subtilis*, *Staphylococcus aureus*, and *Escherichia coli*. The filter paper disc method was used to test for antibacterial activity. A crude extract made from the bryozoan *Bugula pacifica* inhibited the growth of two marine isolates, as well as *B. subtilis*, *S. aureus*, and *E. coli*. A crude extract made from the bryozoan *Tricellaria occidentalis* inhibited the growth of *B. subtilis*. Preliminary scanning electron microscopy data indicate that *Tricellaria occidentalis* had higher densities of surface bacteria than *Bugula pacifica*. This inverse relationship between antibacterial activity and surface fouling may indicate an antifouling role for these bryozoan secondary metabolites. The presence of antibacterial compounds may allow bryozoans to manipulate the microbial film growing on them, and may influence the types of organisms that are able to settle near or on them. The ability to manipulate microbial films may also enable bryozoans to make the substrate nearby more suitable for the settlement of their own larvae.

Introduction

In the marine environment, most surfaces are eventually colonized by sessile organisms such as bacteria, diatoms, protozoans, algae, and invertebrates. However, the surfaces of many of these organisms remain remarkably free of epibionts. This may be due to adaptations to prevent fouling. Possible antifouling mechanisms include mechanical, physical, and chemical defense mechanisms,which may be used alone or combined (Wahl, 1989). This present study was concerned with the chemical defenses of two local, marine bryozoans.

Bryozoans (Ectoprocta) are sessile, colonial, filter-feeding organisms widely distributed throughout the world's marine and freshwater environments. Many bryozoans are common fouling organisms on marine facilities. There are about 4,000 extant species most of which are marine. The class Gymnolaemata encompasses two orders; Ctenostomata and Cheilostomata comprising 3,000 or more living species (Ryland, 1970).

Many marine invertebrates, including sponges (Thompson et al., 1985; Becerro et al., 1994), ascidians (Davis, 1991), jelly fish, sea anemones, bryozoans, and corals (Bhakuni and Jain, 1990) produce secondary metabolites that have antibacterial properties. Study of the antibacterial properties of these substances is unevenly spread across the taxonomic groups. There is a large amount of literature on sponges, less on ascidians and cnidarians, and even less on bryozoans. However, during the past decade, a number of secondary metabolites from marine bryozoans have been isolated and identified. With a few exceptions, the natural products identified from bryozoans so far are either alkaloids, sterols, or bryostatins (Pettit et al., 1982; Anthoni et al., 1990; Morris and Prinsep, 1996; Newman, 1996). Some of the alkaloids have been found to confer antibiotic activity to the bryozoans that produce them. For example: a tetrapyrrole alkaloid isolated from *Bugula dentata* is antimicrobial against Gram-positive and Gram-negative bacteria (Matsunaga et al., 1986); a flustramine alkaloid isolated from *Flustra foliaceae* L. showed strong activity against the bacterium *Bacillus subtilis* (Wright, 1984); antibacterial alkaloids have been isolated from *Phidolopora pacifica* (Tischler et al., 1986); and amathamide alkaloids produced by *Amathia wilsoni* are antibacterial (Walls et al., 1993). Antibacterial secondary metabolites have been found in bryozoans from Tasmania (Walls et al., 1993), the Mediterranean (Uriz et al., 1991), south India (Nair, 1993), the United Kingdom (Al-ogily and Knight-Jones, 1977), Japan (Matsunaga et al., 1986), Scandinavia (Wright, 1984), and the west coast of Canada (Tischler et al., 1986). To date, bryozoans from northern Puget Sound have not been assayed for antibacterial secondary metabolites.

© 1998 by the Northwest Scientific Association. All rights reserved.

Once it is known that an animal such as a bryozoan contains antibacterial secondary metabolites the question arises of how these secondary metabolites affect the ecology of the animal. Antibiotic compounds may allow bryozoans to manipulate the composition of the bacterial film in their immediate vicinity. This could provide the bryozoans with some control over the types of organisms that are able to settle around them or on them (Al-ogily and Knight-Jones, 1977; Uriz et al., 1991; Walls et al., 1993) or may make the substrate more suitable for the settlement of bryozoan larvae (Brancato and Woolacott, 1982; Maki et al., 1989) or less suitable for the settlement of larvae from bryozoan competitors (Maki et al., 1989; Kon-ya et al., 1994).

The bryozoans, *Bugula pacifica* and *Tricellaria occidentalis*, were collected from northern Puget Sound and tested for the presence of antibacterial secondary metabolites. If these compounds were present, their antibacterial properties were measured along with the population of bacteria on the surface of the colonies. The hypothesis tested was that bryozoans which exhibited antibacterial activity would have a lower density of bacteria on their surfaces than bryozoans that did not contain antibacterial secondary metabolites.

Methods

Specimen collection

Erect bryozoans with little or no calcification of the zooecia were collected for this research, because they are easier to extract. Suitable species were found on buoys at two local marinas. On 23 July, 28 July, 4 August, 13 August, and 20 August 1995, *Bugula pacifica* (Figure 1) colonies were collected from the bottom of buoys in Cap Sante Marina, Anacortes, Washington (48° 30' N, 122° 40' W, Figure 2). These collections were made a week apart so as to determine if the concentration of antibacterial compounds in *B. pacifica* changes over time and if the number of bacteria growing on its surfaces changes over time. On 25 August 1995, *B. pacifica* colonies were collected from the bottom of buoys in Point Hudson Marina, Port Townsend, Washington (48° 10' N, 122° 50' W, Figure 2). On 23 July 1995, another suitable bryozoan species, *Tricellaria occidentalis* (Figure 3), was found by snorkeling during a spring low tide at Larrabee State Park (48° 40' N, 122° 30' W, Figure 2). Colonies of this bryozoan were collected from a rock wall. The population of *T. occidentalis* was not large enough for multiple collections.

Back at the laboratory, a dissecting microscope was used to view each bryozoan colony, and fouling organisms were removed using forceps. During this procedure, the bryozoans were kept in cold sea water. After this cleaning procedure, a few colonies from each collection were placed in 95% ethanol for species identification and scanning electron microscope work. The sea water was then drained off the remaining colonies, and they were stored at -20 °C until extracted.

Bacteria used in assays

Twenty-nine strains of marine bacteria were cultured from sea water collected from Cap Sante Marina and Larrabee State Park on 13 August 1995. The water was collected close to where the bryozoan colonies were found using sterile polycarbonate containers, which were opened under water to collect the water samples. The water samples were transported to the lab in a cooler. 10^{-1}, 10^{-2}, and 10^{-3} dilutions were made from each water sample using sterile Bacto Marine Broth 2216 (Difco). 0.1 ml of each dilution were plated on Bacto Marine Agar 2216 (Difco). The plates were incubated in the dark at room temperature, and within two to four days, individual colonies formed. The 10^{-2} dilution yielded the most isolated colonies. The colonies were initially characterized by their size, morphology, growth rate, and color. The individual colonies were then plated, tested for purity and characterized by Gram stain, cell size, and cell morphology. Using hanging drop slides, motility was determined only for the bacteria used in the antibacterial assays. The bacteria were maintained in Bacto Marine Broth 2216 and on slants of Bacto Marine Agar 2216. Five strains of marine bacteria were randomly selected from the 29 marine isolates for use in the antibacterial assays (Table 1). The sixth isolate used, Larrabee State Park 9, was chosen because it was the only Gram-positive isolate.

Four commercial cultures were also used in the antibacterial assays. They were chosen for their Gram stain. *Bacillus subtilis* and *Staphylococcus aureus* are Gram-positive and *Escherichia coli* and *Vibrio anguillarum* are Gram-negative. *V. anguillarum* was also chosen, because it is a

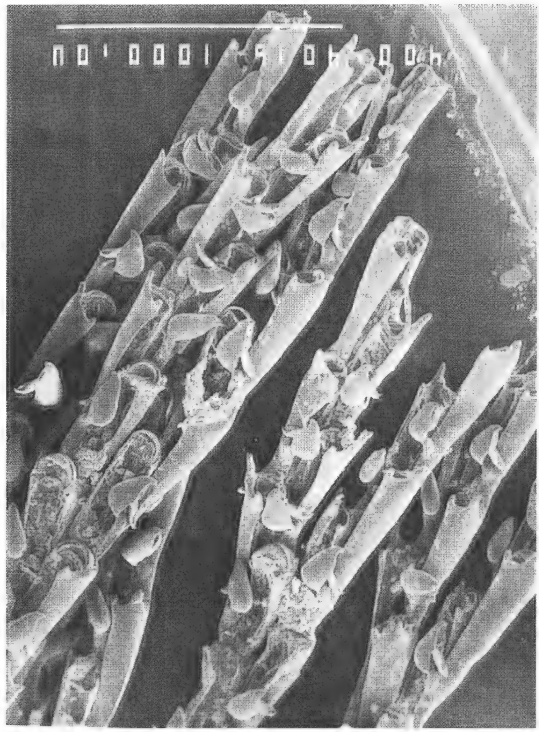


Figure 1. Scanning electron micrograph of *Bugula pacifica*. The scale bar is 1 mm and the magnification is X40.

marine bacterium. The nonmarine cultures were maintained in Nutrient Broth (Difco) and on Nutrient Agar (Difco) slants, and the *V. anguillarium* was maintained in Bacto Marine Broth 2216, and on Bacto Marine Agar 2216 slants.

Extraction

A preliminary extraction indicated that the samples of *Bugula pacifica* collected over time from Cap Sante Marina were too small to detect changes in antibacterial activity over time, so those samples were combined for extraction. The colonies were ground in liquid nitrogen and then lyophilized. During the lyophilization, the containers with the ground bryozoan samples were placed in liquid nitrogen, because the vacuum produced by the lyophilizer was not sufficient to prevent the samples from melting. Each sample was extracted overnight three times with distilled dichloromethane (DCM) in a proportion of 0.1 g dry weight in 10 ml of solvent (Walls et al., 1993; Becerro et al., 1994). The crude extracts were evaporated under reduced pressure and the residue was weighed. The residues were stored at -20 °C until tested for antibacterial activity.

Antibacterial testing

For antibacterial testing, 3 ml of DCM were added to the Cap Sante Marina extract of *Bugula pacifica*, and 2 ml were added to the Larrabee State Park extract of *Tricellaria occidentalis* and to the Point Hudson Marina extract of *Bugula pacifica*. Less DCM was added to the last two samples, because fewer colonies used were to make the extracts. This procedure should have maximized the antibacterial activity of the extracts and should have equalized the concentration of antibacterial compounds in all three extracts. DCM is highly volatile, so 2 ml were the minimum of DCM that was needed to soak filter paper discs for all three

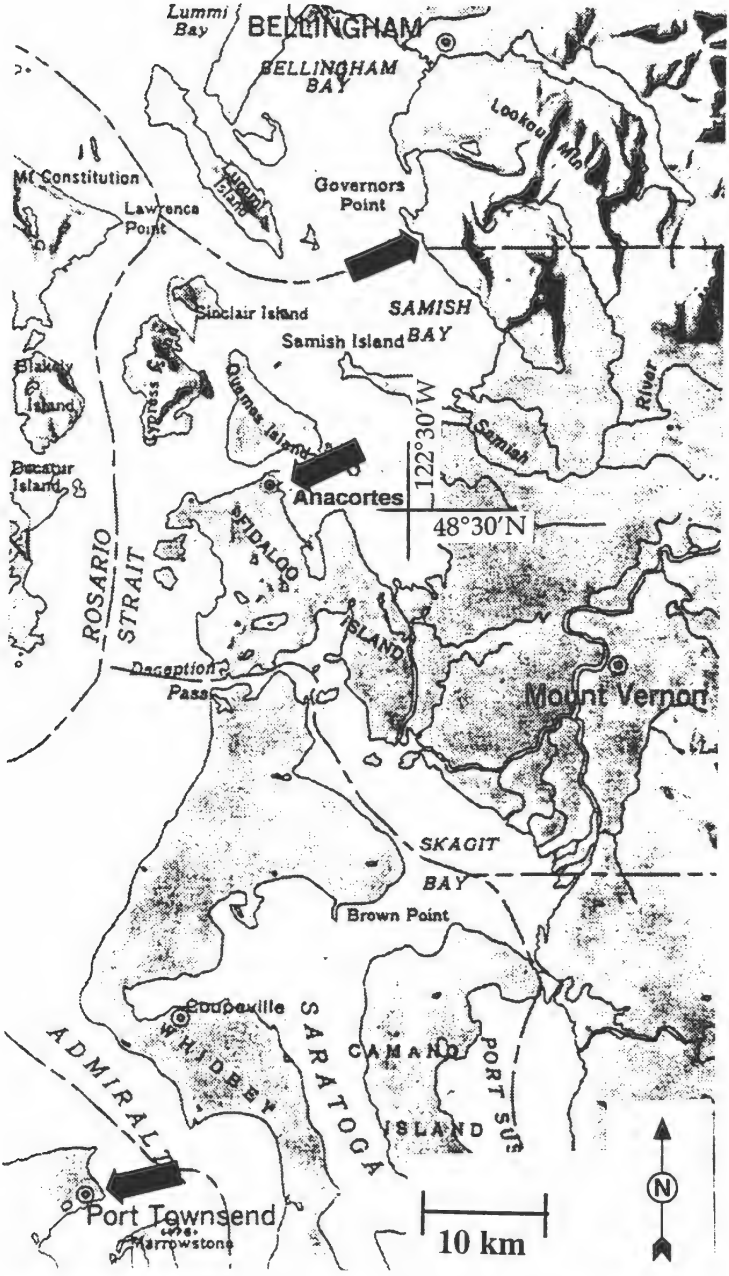


Figure 2. Map showing the three collection sites in northwest Washington State. The northernmost site is a small harbor at Larrabee State Park, the second site is Cap Sante Marina, Anacortes, and the southernmost site is Point Hudson Marina, Port Townsend. Collection sites are marked with arrows.

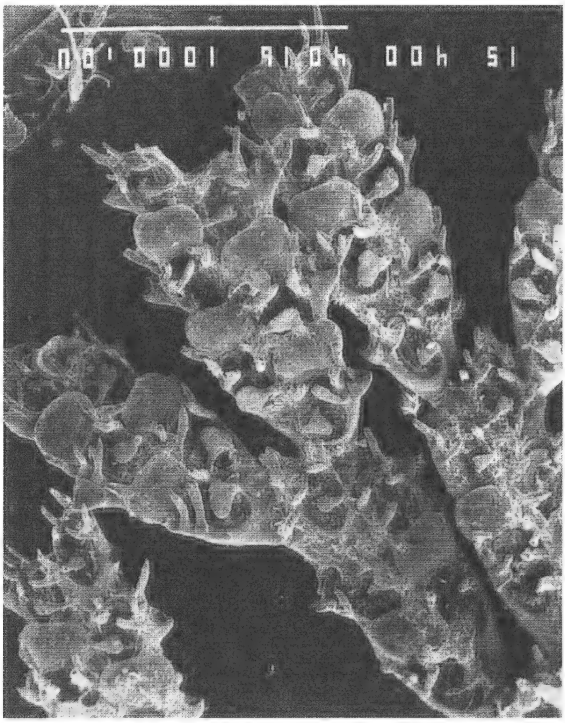


Figure 3. Scanning electron micrograph of *Tricellaria occidentalis*. The scale is 1 mm and the magnification is X40.

replicates. Each extract was tested against the six strains of marine bacteria and against the four commercial cultures. The antibacterial assays were performed using the filter paper disc method developed by Berquist and Bedford (1978). A lawn of each species of bacteria was spread on petri plates prepared with Bacto Marine Agar 2216. Four filter paper discs (6 mm diameter) were impregnated with 5 µl of extract, and one control disc was impregnated with 5 µl of DCM. The discs were placed on the bacterial lawns, and the plates were incubated for 24 h at 24 °C. Three replicates were run, and the average diameter of zones of inhibition (including the disc) was recorded.

Scanning electron microscopy

Bryozoan colonies of *Tricellaria occidentalis* from Larrabee State Park and the weekly collections of *Bugula pacifica* colonies from Cap Sante Marina were examined at the University of Washington's Friday Harbor Laboratories using a JEOL JSM 35 scanning electron microscope (SEM). The colonies were stored in 95% ethanol for 5 months at room temperature before being examined by SEM. For the SEM work, the colonies were then dehydrated through an alcohol series, treated with hexamethyldisalizane for 15 min., air dried, mounted on stubs with double sided-tape and silver paint, and sputter coated with gold and palladium. The magnification of the SEM was adjusted to produce a display size of 100 μm^2. The number of bacteria and their cell morphology was recorded on 12 spine tips and 12 zooecia on the weekly bryozoan samples of *Bugula pacifica* from Cap Sante Marina, and they were recorded on 12 spine tips and 12 scuta on the bryozoan colonies of *Tricellaria occidentalis* from Larrabee State Park. Therefore, the total area viewed per location on each colony was 1200 μm^2.

Bryozoan species identification

An initial identification of each species was made as the bryozoans were collected. Colonies which

TABLE 1. Marine bacteria isolated from water at Cap Sante Marina and Larrabee State Park. The isolates were characterized according to Gram stain, size, and morphology. The isolates were characterized according to Gram stain, size, and morphology. The isolates used in the antibacterial assays were also tested for motility, and are marked with an asterisk (*). Size refers to length if bacillus or spirillum and to diameter if coccus.

Collection site	Stain no.	Gram stain	Size (μm)	Morphology	Motility
Cap Sante Marina	1*	–	2.5-5	bacillus	+
	2*	–	4	bacillus	+
	3	–	0.5	bacillus	n.a.
	4	–	2.5-7.5	coccus	n.a.
	5	–	1.25	coccus	n.a.
	6	–	2.5	coccus	n.a.
	7*	–	6.25	bacillus	–
	8	–	2.5	bacillus	n.a.
	9	–	2.5	coccus	n.a.
	10	–	2.5	bacillus	n.a.
	11*	–	1.88	bacillus	+
	12	–	2-5	bacillus	n.a.
	13	–	3	bacillus	n.a.
	14	–	1	bacillus	n.a.
	15	–	2.5	bacillus	n.a.
	16*	–	2.5	spirillum	+
	17	–	1.88	coccus	n.a.
Larrabee State Park	1	–	2.5-5	bacillus	n.a.
	2	–	1.25	bacillus	n.a.
	3	–	2.5	bacillus	n.a.
	4	–	2.5	bacillus	n.a.
	5	–	2.5	bacillus	n.a.
	6	–	1.88	coccus	n.a.
	7	–	1.25	coccus	n.a.
	8	–	2.5	bacillus	n.a.
	9*	+	2.5	bacillus	–
	10	–	3.5	coccus	n.a.
	11	–	2.5	coccus	n.a.
	12	–	2.5	coccus	n.a.

had been stored in ethanol were later verified to species using keys by Bergey and Denning (1987), Gordon (1986), and Osburn (1950). Scanning electron micrographs were also used in keying out the species.

Numerical methods

Zones of inhibition were used only as an indication of antibacterial activity, and no attempt was made to compare them using statistics, because the chemical nature of the bryozoan secondary metabolites tested is unknown and presumably different. Therefore, they would diffuse in agar at different rates and to different extents. Thus, zones of inhibition cannot be used to compare directly the potencies of different chemical compounds.

Because the number of bryozoan colonies used to estimate the density of surface bacteria was small, parametric statistics were not used to analyze the data. Standard errors were used to provide an indication of the precision of the estimation of the population mean (Sokal and Rohlf, 1981; Zar, 1974). Thus, counts of bacteria are reported as means with standard errors, and if the error bars in the histograms reported here do not overlap, the means are probably different.

Results

At both Cap Sante Marina and Point Hudson Marina, *Bugula pacifica* was found on the bottom of buoys which were in the early phases of fouling. *B. pacifica*'s main competitor for space on the buoys was the compound ascidian *Distaplia*

occidentalis, which was the only animal observed to overgrow *B. pacifica*. The *B. pacifica* colonies collected from Cap Sante Marina on 21 August were fouled with algae and had many caprellid amphipods living on them. There were also many caprellid amphipods living on the *B. pacifica* colonies collected from Point Hudson Marina on 25 August. *Tricellaria occidentalis*, collected at Larrabee State Park, was found attached either directly to a vertical rock face, or to holdfasts of the green alga *Ulva* and the bases of the red alga *Prionitis*, both of which were also attached to the rock face. In general, the colony bases of both bryozoan species had more marine debris on them than the colony tips. The *B. pacifica* colonies were 3-5 cm tall, and the *T. occidentalis* colonies were 1-2 cm tall.

All the marine bacteria isolates used in the antibacterial assays were Gram-negative, except one (Table 1). Their size ranged from 1.88-6.25 μm. Five of the six marine isolates used in the antibacterial assays were bacillus and one was spirillum. Four of the six were motile.

During the extraction of *B. pacifica*, the DCM turned a pea soup green color, and it was cloudy. During the extraction of *T. occidentalis*, the DCM turned a yellowish-green color, but was not cloudy. After the DCM was evaporated off the extracts, the *B. pacifica* residue was oily and green, and the *T. occidentalis* residue was oily and yellowish-brown. The residue from the *B. pacifica* colonies collected from Cap Sante Marina was 0.024 % of the sample dry weight, and the residue from the *B. pacifica* colonies collected from Point Hudson Marina was 0.050 % of the sample dry weight. The residue from the *T. occidentalis* colonies was 0.026 %. These residue weights are approximate, because some sediment remained in the final extracts, especially in the extracts made from the bryozoans collected at Point Hudson Marina and Larrabee State Park.

The extract made from the *B. pacifica* colonies from Cap Sante Marina inhibited two cultures of marine bacteria: CS 2 and CS 16, and three nonmarine bacteria: *B. subtilis*, *S. aureus*, and *E. coli* (Table 2). The extract made from the *B. pacifica* colonies from Point Hudson Marina inhibited one marine bacterium: CS 16, and two nonmarine bacteria: *B. subtilis* and *S. aureus*. The extract made from the *T. occidentalis* colonies inhibited the nonmarine bacterium *B. subtilis*.

From the SEM analysis, the growth of surface bacteria on *B. pacifica* varied over time. The mean surface density of bacteria on *B. pacifica* on 28 July 1995 was 0.7 ± 0.2 bacteria/100 μm^2 (Table 3). The density increased to 5.0 ± 1.4 bacteria/100 μm^2 on 4 August 1995, and it decreased slightly to 4.4 ± 0.8 bacteria/100 μm^2 on 13 August 1995. By 21 August 1995, the mean surface density of bacteria on the surface of *B. pacifica* had decreased to 2.3 ± 0.8 bacteria/100 μm^2.

The density of surface bacteria on *T. occidentalis* (collected on 23 July 1995) was three times greater than that found on the *B. pacifica* colonies (collected on 28 July 1995). *T. occidentalis* had a mean surface density of bacteria of 2.1 ± 0.8 bacteria/100 μm^2 compared to a mean surface density of bacteria of 0.7 ± 0.2 bacteria/100 μm^2 on *B. pacifica* (Table 3). In both bryozoan species, the mean surface density of bacteria on the spine

TABLE 2. Assay results for crude extracts from two species of marine bryozoans collected in July and August, 1995 in northern Puget Sound, Washington. The assay for antibacterial activity of extracts was scored doubly positive (++) if the zone of inhibition was between 1 and 2 mm from the edge of the disc, positive (+) if the zone was ≤ 1 mm from the edge of the disc, and negative (–) if there was no inhibition of bacterial growth. CS—Cap Sante Marina; PH—Point Hudson Marina; LSP—Larrabee State Park.

	Marine bacteria						Nonmarine bacteria			
Bryozoan and (collection site)	CS 1	CS 2	CS 7	CS 11	CS 16	LSP 9	*Vibrio anguillarum*	*Bacillus subtilis*	*Staphylococcus aureus*	*Escherichia coli*
Bugula pacficia (CS)	–	++*	–	–	+	–	–	++	+	+
Bugula pacifica (PH)	–	–	–	–	+*	–	–	+	+	+
Tricellaria occidentalis (LSP)	–	–	–	–	–	–	+	–	–	

*Zone of inhibition only seen in the third replicate.

TABLE 3. The density of surface bacteria on different areas of *Bugula pacifica* and *Tricellaria occidentalis*. Counts were made using scanning electron microscopy. Values are the mean number of bacteria/100 μm² with standard errors.

Species		Location	Count	Filamentous	Mean Cocci	Mean Bacilli
B. acificia	28-Jul-95	Spine tip	12	no	0	
		Zooecium	12	no		
	4-Aug-95	Spine tip	12	no		
		Zooecium	12	no		
	13-Aug-95	Spine tip	12	yes		
		Zooecium	12	yes		
	21-Aug-95	Spine tip	12	yes		
		Zooecium	12	yes		
T. occidentalis	23-Jul-95	Spine tip	12	no	0	
		Scutum	12	yes		

tips was lower than that on the zooecium or scutum (Table 3).

The growing tips of the branches of *B. pacifica* usually had a lower surface density of bacteria than the bases of the branches. The growing tips of *T. occidentalis* did not have any bacteria on them. In *B. pacifica*, the distance from the growing tip to the base of a branch is 3-5 mm, and in *T. occidentalis* it is 2 mm (3 zooecia).

Rod-shaped bacteria were the dominant type of bacteria on the surfaces of *B. pacifica* and *T. occidentalis*. They were also the most dominant type of bacteria isolated from the water surrounding the bryozoans. A small amount of filamentous bacteria was observed on the *B. pacifica* colonies on 13 August 1995. By 21 August 21. 1995, there were many more filamentous bacteria present on the colony surface. Filamentous bacteria were also observed on *T. occidentalis*.

Discussion

The results from this study indicate that both *Bugula pacifica* and *Tricellaria occidentalis* do contain antibacterial compounds and that the extracts made from *B. pacifica* exhibited more antibacterial activity than the extract made from *T. occidentalis*. These results are particularly exciting when they are combined with the observation that the surfaces of *B. pacifica* had less bacteria growing on them than the surfaces of *T. occidentalis*, suggesting that *B. pacifica* was possibly more effective in deterring microbial epibionts.

Other researchers have also found an inverse correlation between antimicrobial activity and surface fouling, suggesting that antibacterial activity may help a sessile organism such as a bryozoan prevent the growth of epibionts (McCaffrey and Endean, 1985; Walls et al., 1993). Because space is a limiting resource for benthic organisms, they will often settle on each other (Jackson and Buss, 1975). Studies have shown that a surface film of microorganisms (bacteria being the first to arrive) is often required for the settlement of many fouling invertebrates including hydroids, polychaetes, bivalves, gastropods, barnacles, echinoderms, and bryozoans (MacGinitie and MacGinitie, 1949; Crisp, 1984; Pawlik, 1992). Therefore, preventing the growth of epibionts is important, especially for animals like bryozoans which are filter feeders, because for efficient filtration to occur, the colony surface must be kept clean. Macroepibionts can be especially harmful, because they can deplete incoming water of nutrients if they are also filter feeders, or they may alter current patterns at the colony surface (Wahl and Lafargue, 1990). In addition to promoting larval settlement, microbial films may be deleterious in other ways. They may cause chemical attack of the colony surface by slime mold metabolism, they may promote further fouling by creating attachment points or nutrient-rich microenvironments, or they may form an insulating layer between settling larvae and the toxins produced by the organism (Wahl, 1989).

Kon-ya et al. (1994) showed that an extract made from the bryozoan *Zoobotryon pellucidum* inhibited the settlement of barnacle and mussel larvae. This suggests that, in addition to inhibiting the growth of bacteria, the secondary metabolites produced by bryozoans may directly influence

larval settlement behavior. However, to date, the allelochemicals produced by bryozoans have not been measured in the water surrounding them.

It is possible that *B. pacifica* from Cap Sante Marina showed more antibacterial activity not because it has stronger secondary metabolites, but because the extract made from those colonies was more concentrated. The Cap Sante Marina extract of *B. pacifica* contained about four times as many colonies as the extracts of *B. pacifica* from Point Hudson Marina and *T. occidentalis* from Larrabee State Park. However, the samples of *B. pacifica* from Point Hudson Marina and *T. occidentalis* from Larrabee State Park were approximately the same size, and *B. pacifica* from Point Hudson Marina inhibited more species of bacteria than *T. occidentalis*.

There were two cases where zones of inhibition were only seen in the third replicate (Table 2). This is probably due to the highly volatile nature of DCM; 0.6 ml of each extract were used for the antibacterial assays, but by the time each assay was finished, at least twice that much DCM had evaporated from the extracts. Thus, the extracts became more concentrated over time.

The use of the filter paper disc method to measure the amount of antibacterial activity has its limitations, because lipid soluble compounds in the DCM extract do not diffuse into agar well, and other compounds may diffuse at different rates and amounts. Therefore, this method cannot be used to compare directly the strength of different compounds. Nevertheless, this method is widely used, because it is an easy and accurate method for detecting the antibacterial activity of various compounds (Berquist and Bedford, 1978; Walls et al., 1993).

The number of bacteria on the surface of *B. pacifica* did change over time. However, the decrease in the number of bacteria on August 21 was not expected. On the contrary, an increase in the number of bacteria throughout the sample period was expected. Because it was not possible to test for changes in antibacterial activity over time, we do not know if the changes in the number of bacteria that were observed are linked to variable production of antibacterial compounds by the bryozoan or if they are due to natural, seasonal cycles of bacterial growth.

It is possible that the differential distribution of bacteria between the spine tips, which are above the zooid surface, and the zooecium or scutum is due to a differential distribution of antibacterial compounds within the zooid. However, a more likely explanation is that it is related to zooid morphology. The spine tips are more exposed to water currents than the rest of the zooid. This may make them less suitable for the settlement and growth of bacteria.

The differential distribution of bacteria between the growing tips and more proximal portions of the colony may be due to a differential distribution of antibacterial compounds within the colony. This was shown to be true for the bryozoan *Amathia wilsoni*. In *A. wilsoni*, higher concentrations of antibacterial compounds were measured in the growing tips than in the basal portions of the colony, and samples taken midcolony had intermediate concentrations. The distribution of bacteria on the surface of *A. wilsoni* was patchy and could be related to the distribution of antibacterial compounds within the colony (Walls et al., 1991; Walls et al., 1993). Again, morphology may also be a factor. The growing portions of the colony are more exposed to water currents, and so they may not be favored by bacteria for settlement and growth. Age may be another factor influencing the distribution of bacteria on the colony. Proximal portions of the colony are older, so bacteria have had more time to settle and to grow on these parts of the colony.

We were unable to determine if the bryozoan extracts contained alkaloids. However, in most cases, the secondary metabolites isolated from bryozoans have been found to be alkaloids (Christophersen, 1985; Anthoni et al., 1990; Prinsep and Morris, 1996). It is likely that the active secondary metabolites isolated from *B. pacifica* and *T. occidentalis* have an alkaloid component.

This study initiates efforts to characterize the chemical nature of bryozoans from Pacific Northwest waters and to understand the role of these metabolites. However, much remains to be done. The question of whether or not the concentration of antibacterial compounds in these bryozoans changes over time remains unanswered. Unfortunately, the small size of these animals limits the amount of extract that can be made from them, so a more precise way to measure antibacterial activity than the filter paper disc method may be needed to answer this question. An attempt needs to be made to measure biologically active

secondary metabolites in the water surrounding *B. pacifica* and *T. occidentalis*. This may be possible using a submersible apparatus developed by Coll et al. (1982). The apparatus permits *in situ* sampling of allelochemicals released from sessile marine organisms. It would also be interesting to see if extracts from these bryozoans can inhibit the settlement of larvae from their competitors or perhaps enhance settlement of their own larvae. The active components of the extracts need to be isolated and characterized using HPLC. More extensive SEM work would be useful, especially if counts of bacteria were made on colonies collected over a longer period of time. Studies of this type have the potential to lead to a greater understanding of the ecology of fouling communities. The presence of chemical defenses within even a small proportion of sessile organisms in a community may influence the community structure by influencing patterns of grazing, larval settlement, and adult interrelationships.

Acknowledgements

We are grateful to Drs. E. Peele and D. Williams, Western Washington University, for their comments on this manuscript. Dr. G. Prody, Western Washington University, helped with the lyopholizer. S. Schwinge and Dr. W. Jaeckle, University of Washington Friday Harbor Labs, helped with the SEM work. Dr. J. Walls, University of Tasmania, and Dr. D. Newman, National Cancer Institute, provided invaluable advice on bryozoan extraction methods. This research was supported by the Charles and June Ross Graduate Fellowship, the Department of Biology at Western Washington University, and the Northwest Science Association.

Literature Cited

Al-ogily, S. M. and E. W. Knight-Jones. 1977. Antifouling role of antibiotics produced by algae and bryozoans. Nature 265:728-729.

Anthoni, U., P. H. Nielsen, M. Pereira, and C. Christophersen. 1990. Bryozoan secondary metabolites: a chemotaxonomical challenge. Comparative Biochemistry and Physiology 96(3):431-437.

Becerro, M. A., N. I. Lopez, X. Turon, and M. J. Uriz. 1994. Antimicrobial activity and surface bacterial film in marine sponges. Journal of Experimental Marine Biology and Ecology 179:195-205.

Bergey, A. and D. Denning. 1987. Phylum Bryozoa (Ectoprocta), p. 423-446. *In* E. N. Kozloff, ed. Marine invertebrates of the Pacific Northwest. University of Washington Press, Seattle.

Berquist, P. R. and J. J. Bedford. 1978. The incidence of antibacterial activity in marine Demospongiae: systematic and geographic considerations. Marine Biology 46:215-221.

Bhakuni, D. S. and S. Jain. 1990. Bioactive metabolites of the marine invertebrates: part I - sponges, jelly fish, sea anemones, corals and bryozoans. Journal of Scientific and Industrial Research 49:330-349.

Brancato, M. S. and R. M. Woolacott. 1982. Effect of microbial films on settlement of bryozoan larvae (*Bugula simplex*, *Bugula stolonifera*, and *Bugula turrita*). Marine Biology 71:51-56.

Coll, J. C., B. F. Bowden, D. M. Tapiolas, and W. C. Dunlap. 1982. In situ isolation of allelochemicals released from soft corals (Coelenterata: Octocorallia): A totally submersible sampling apparatus. Journal of Experimental Marine Biology and Ecology 60:293-299.

Christophersen, C. 1985. Marine alkaloids, Vol. 24, Ch. 2. *In* A. Brossi, ed. The alkaloids: chemistry and pharmacology. Academic Press, Inc., New York.

Crisp, D. J. 1984. Overview of research on marine invertebrate larvae, 1940-1980, p. 103-126. *In* J. D. Costlow and R. C. Tipper, eds. Marine biodeterioration: an interdisciplinary study. Naval Institute Press, Annapolis, Maryland.

Davis, A. R. 1991. Alkaloids and ascidian chemical defenses: evidence for the ecological role of natural products from *Eudistoma olivaceum*. Marine Biology 111:375-379.

Gordon, D. P. 1986. The marine fauna of New Zealand: Bryozoa: Gymnolaemata (Ctenostomata and Cheilostomata Anasca) from the western South Island continental shelf and slope. New Zealand Oceanographic Institute Memoir 95, Wellington.

Jackson, J. B. C. and L. Buss. 1975. Allelopathy and spatial competition among coral reef invertebrates. Proceedings of the National Academy of Science, USA 72 (12):5160-5163.

Kon-ya, K., N. Shimidzu, K. Adachi, and W. Miki. 1994. 2,5,6-Tribromo-1-methylgramine, an antifouling substance from the marine bryozoan *Zoobotryon pellucidum*. Fisheries Science 60(6):773-775.

MacGinitie, G. E. and N. MacGinitie. 1949. Natural history of marine animals. McGraw-Hill Book Co., New York.

Maki, J. S., D. Rittschof, A. R. Schmidt, A. G. Snyder, and R. Mitchell. 1989. Factors controlling attachment of bryozoan larvae: A comparison of bacterial films and unfilmed surfaces. Biol. Bull. 177:295-302.

McCaffrey, E. J. and R. Endean. 1985. Antimicrobial activity of tropical and subtropical sponges. Marine Biology 89:1-8.

Matsunaga S., N. Fusetani, K. Hashimoto. 1986. Bioactive marine metabolites. VIII. isolation of an antimicrobial blue pigment from the bryozoan *Bugula dentata*. Experientia 42:84.

Morris, B. D. and M. R. Prinsep. 1996. Metabolites from the marine ctenostome *Amathia wilsoni*, p. 199-205. In D. P. Gordon, A. M. Smith, and J. A. Grant-Mackie, eds., Bryozoans in space and time. Proc. 10th International Bryozoology Association Conference, NIWA, Wellington, N.Z.

Nair, P. S. R. 1993. Antibacterial activity of the bryozoan *Electra bellula* (Hincks). Indian Journal of Medical Research 97:85-86.

Newman, D. J. 1996. Keynote Address: Bryostatin—from bryozoan to cancer drug, p. 9-17. *In* D. P. Gordon, A. M. Smith, and J. A. Grant-Mackie, eds., Bryozoans in space and time. Proc. 10th International Bryozoology Association Conference, NIWA, Wellington, N.Z.

Osburn, R. C. 1950. Bryozoa of the Pacific Coast of America: part 1, Cheilostomata-Anasca. University of Southern California Press, Los Angeles.

Paech, K. and M. V. Tracey, eds. 1955. Modern methods of plant analysis. Springer-Verlag, Berlin.

Pawlik, J. R. 1992. Chemical ecology of the settlement of benthic marine invertebrates. Oceanography and Marine Biology Annual Review 30:273-335.

Pettit, G. R., D. Sengupta, P. M. Blumberg, N. E. Lewin, J. M. Schmidt, A. S. Kraft. 1982. Structural modifications of bryostatin 2. Anti-Cancer Drug Design. 7:101-113.

Prinsep, M. R. and B. D. Morris. 1996. Secondary metabolites from New Zealand marine Bryozoa, p. 227-235. In D. P. Gordon, A. M. Smith, and J. A. Grant- Mackie, eds., Bryozoans in space and time. Proc. 10th International Bryozoology Association Conference, NIWA, Wellington, N.Z.

Ryland, J. S. 1970. Bryozoans. Hutchinson University Library, London.

Received 30 July 1997
Accepted for publication 16 December 1997

Sokal, R. R., and F. J. Rohlf. 1981. Biometry: The principles and practice of statistics in biological research, 2nd edition. W. H. Freeman and Company, New York.

Thompson, J. E., R. P. Walker, and D. J. Faulkner. 1985. Screening and bioassays for biologically-active substances from forty marine sponge species from San Diego, California USA. Marine Biology 88:11-21.

Tischler, M., S. W. Ayer, and R. J. Andersen. 1986. Nitrophenols from northeast Pacific bryozoans. Comparative Biochemistry and Physiology 84B(1):43-45.

Uriz, M. J., D. Martin, X. Turon, E. Ballesteros, R. Hughes, C. Acebal. 1991. An approach to the ecological significance of chemically mediated bioactivity in Mediterranean benthic communities. Marine Ecology Progress Series 70:175-188.

U.S. Geologic Survey. State of Washington [map]. 1:500,000. Washington, D.C.: USGS, 1964.

Wahl, M. 1989. Marine epibiosis. I. Fouling and antifouling: some basic aspects. Marine Ecology Progress Series 58:175-189.

Wahl, M. and F. Lafargue. 1990. Marine epibiosis. II. Reduced fouling on *Polysyncraton lacazei* (Didemnidae, Tunicata) and proposal of antifouling potential index. Oecologia 82:275-282.

Walls, J. T., A. J. Blackman, and D. A. Ritz. 1991. Distribution of amathamide alkaloids within single colonies of the bryozoan *Amathia wilsoni*. Journal of Chemical Ecology 17(9):1871-1881.

Walls, J. T., D. A. Ritz, and A. J. Blackman. 1993. Fouling, surface bacteria and antibacterial agents of four bryozoan species found in Tasmania, Australia. Journal of Experimental Marine Biology and Ecology 169:1-13.

Wright, J. L. C. 1984. A new antibiotic from the marine bryozoan *Flustra foliaceae*. Journal of Natural Products 47(5):893-895.

Zar, J. H. 1974. Biostatistical Analysis. Prentice-Hall, Inc., Englewood Cliffs, N. J.

Matthew W. McDonald and **Kerry P. Reese,** Department of Fish and Wildlife Resources, University of Idaho, Moscow, Idaho 83844

Landscape Changes within the Historical Distribution of Columbian Sharp-tailed Grouse in Eastern Washington: Is There Hope?

Abstract

Landscape changes within the historical distribution of Columbian sharp-tailed grouse (*Tympanuchus phasianellus columbianus*) in eastern Washington were assessed and analyzed to predict the most suitable areas for habitat improvement. The most significant changes involved the decline and fragmentation of grassland and sagebrush (*Artemisia* spp.) cover types, and the emergence of the cropland/hay/pasture cover type. Grasslands decreased from 25% to 1% of the landscape, while mean patch size declined from 3,765 ha to 299 ha. Sagebrush decreased from 44% to 16% of the landscape and has become extremely fragmented. Grasslands and sagebrush are two of the habitats most frequently used by Columbian sharp-tailed grouse. Conversion of most grassland and sagebrush to cropland is responsible for the decline of sharp-tailed grouse, and has resulted in disjunct populations. Future efforts to expand the range and number of birds should be centered around the Dyer Hill and Colville populations due to current landscape characteristics and population sizes.

Introduction

Columbian sharp-tailed grouse (*Tympanuchus phasianellus columbianus*) were once considered one of the most abundant and well known gamebirds in eastern Washington (Bendire 1892, Yocom 1952). This subspecies of sharp-tailed grouse inhabited steppe, meadow-steppe, and shrub-steppe communities (Daubenmire 1988). Historically, population numbers were greatest in grassland (steppe and meadow-steppe) habitat (Bendire 1892, Yocom 1952, Jewett et al. 1953), the majority of which occurred on the Palouse Prairie, in southeastern Washington. Sharp-tailed grouse occupied sagebrush (shrub-steppe) regions of its range in lesser numbers.

By 1920, approximately 80% of the Palouse was under cultivation (Buss and Dziedzic 1955). Sharp-tailed grouse nested in the stubble of wheat fields until burning and plowing stubble became common practices by 1910 (Yocom 1952, Buss and Dziedzic 1955). Within a span of 10 years (1910 - 1920) sharp-tailed grouse decreased from being abundant to scarce in southeastern Washington (Buss and Dziedzic 1955).

Currently, Columbian sharp-tailed grouse occupy < 11% of their historic range and are estimated to number fewer than 1000 birds in Washington (Idaho Department Fish and Game, pers. comm.). Moreover, the situation is dire because there are only four core populations that are relatively moderate in size (≥ six leks), and populations are disjunct with genetic flow unlikely due to habitat fragmentation.

Habitat fragmentation may have substantial effects on population stability and persistence. In the past, ecologists considered most populations and associated ecological processes only on local spatial scales (Dunning et al. 1992). However, the emergence of metapopulation theory (Gilpin and Hanski 1991), patch dynamics theory (Pickett and White 1985), and landscape ecology (Forman and Godron 1986), emphasized the importance of the effects of landscape level changes on vertebrate distributions and population dynamics.

The objectives of this paper are to 1) describe changes in composition and configuration of patches within the landscape corresponding to historical distribution of Columbian sharp-tailed grouse within Washington, and 2) determine future areas most suitable for habitat improvement given the current vegetation pattern and core grouse population distribution.

Study Area

The study area is delineated by the historical distribution of Columbian sharp-tailed grouse within Washington (Figure 1), and ranges from the Canadian border south to Oregon, east to Idaho, and west to the eastern Cascade foothills (Jewett et al. 1953). Our map differs slightly from that of Miller and Graul (1980) by being a minor, recent

© 1998 by the Northwest Scientific Association. All rights reserved.

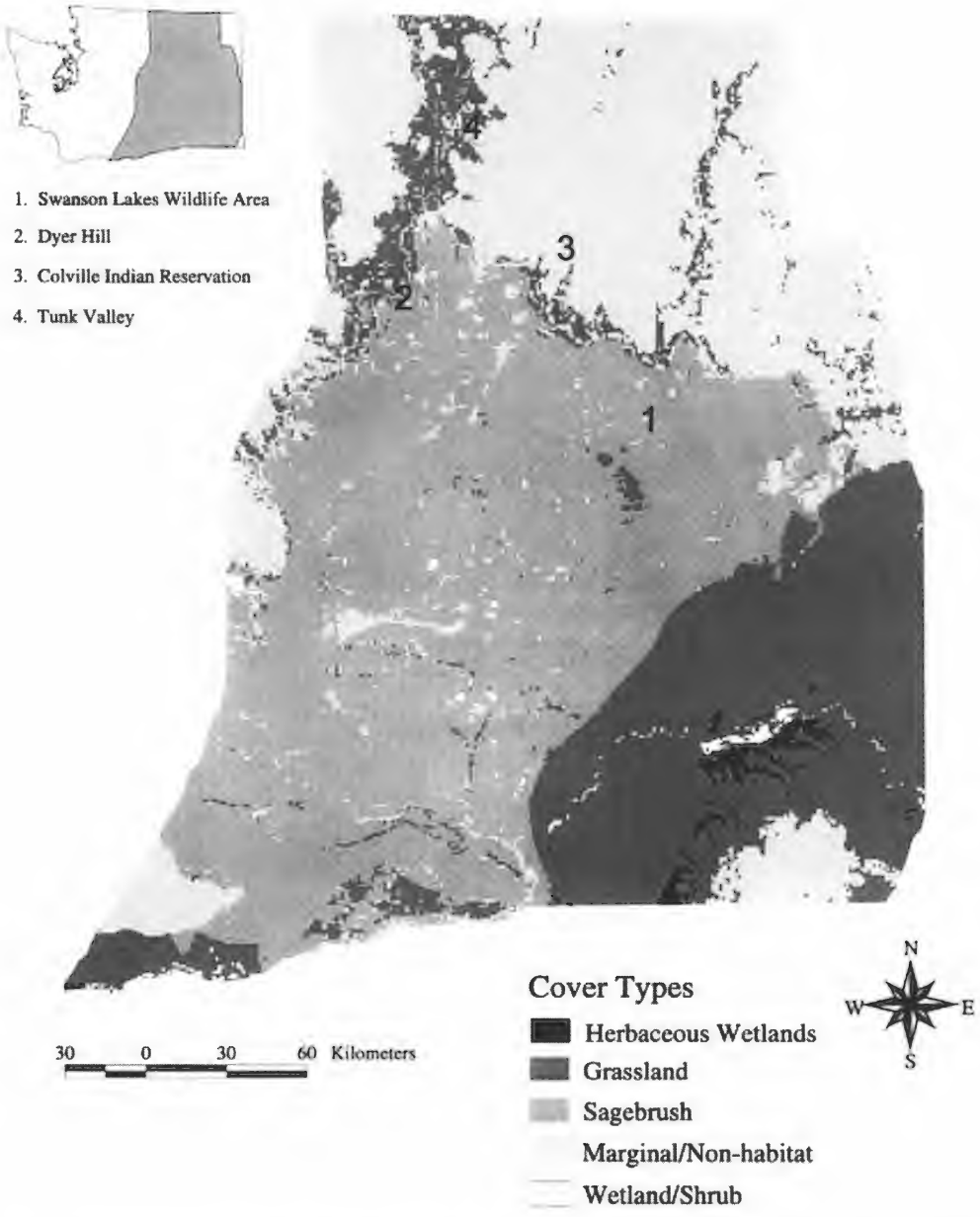


Figure 1. Historical (circa 1900) cover type map corresponding with the historical distribution of Columbian sharp-tailed grouse in Washington (Washington Department of Fish and Wildlife 1995).

refinement by the Washington Department of Fish and Wildlife (1995). This expansive area was not a continuous range, but contained scattered populations in areas of suitable habitat.

Historically, the southeastern part of the study area was dominated by grassland consisting of bluebunch wheatgrass (*Agropyron spicatum*) and fescue (*Festuca* spp.) grasses. Grassland also occurred along the major rivers. Sagebrush communities, consisting of big sagebrush (*Artemisia tridentata*), three-tip sagebrush (*A. tripartita*), and rigid sagebrush (*A. rigida*), occupied the central and southwestern portions of the study area. Coniferous forests existed mainly in the northern portion of the study area.

Four core populations of sharp-tailed grouse occur in Washington (Figure 1). One population exists on Swanson Lakes Wildlife Area and surrounding land, located in the channeled scablands. The majority of this area is sagebrush with scattered areas of former agricultural lands currently in the Conservation Reserve Program (CRP). The second population occurs in the vicinity of Dyer Hill. The general area is mostly cropland, however, there are areas of remnant sagebrush and a state wildlife area (Central Ferry Canyon) created as a refuge for sharp-tailed grouse. The third population, on the Colville Indian Reservation, inhabits steppe habitat around the town of Indian Agency. This area has the most extensive grassland and riparian habitat of the core population areas and has the largest population of Columbian sharp-tailed grouse in Washington. The fourth population occurs in the Tunk Valley, where sagebrush dominates the valley, surrounded by forest. Cropland and CRP patches are also part of the habitat mosaic. There are also birds disjunct from the core populations. Due to the small number of birds and their relative isolation, they are not considered to contribute to the overall population (Washington Department of Fish and Wildlife 1995).

Methods

Geographic information systems software, ARC/INFO and ARCView, were used to generate maps of historical (circa 1900) and current (1990) vegetation patterns coinciding with historical range of Columbian sharp-tailed grouse in Washington (Washington Department of Fish and Wildlife 1995). Historical and current vegetation maps were produced using coverages from the Interior Columbia Basin Ecosystem Management Project (ICBEMP) Historical and Current Cover Type Maps, respectively (Quigley et al. 1996). These cover type maps were intended for use at the regional level (> 300,000 ha) (J. P. Menakis, USDA Forest Serv. Intermountain Fire Sciences Lab, pers. comm.) and were considered appropriate for landscape level analysis. Both the historical and current vegetation maps have a 100-ha pixel resolution, adequate for Columbian sharp-tailed grouse because their seasonal home ranges are larger than 100 ha both for winter and summer (Gratson 1988, Northrup 1991, Ulliman 1995). Grassland, sagebrush and herbaceous wetlands are of primary importance to Columbian sharp-tailed grouse during breeding and brood-rearing, while deciduous trees and shrubs in riparian and mountain shrub cover types are used for both food and cover in winter (Marks and Marks 1988, Ulliman 1995, Washington Department of Fish and Wildlife 1995). Cover types from ICBEMP data were reduced to five categories by combining similar cover types used by Columbian sharp-tailed grouse. For example, big sagebrush, mountain big sagebrush (*A. t. vaseyana*), and low sagebrush (rigid sagebrush) cover types were combined into one cover type "sagebrush", and fescue/bunchgrass and Agropyron bunchgrass were combined into the "grassland" cover type. The marginal/non-habitat cover type consists of cover types that sharp-tailed grouse may use infrequently (e.g., bitterbrush (*Purshia tridentata*)/bluebunch wheatgrass, juniper (*Juniperus* spp.)/sagebrush, salt desert shrub, etc.), in addition to cover types that Columbian sharp-tailed grouse rarely use (e.g., coniferous forests). Cover types potentially used as winter habitat (riparian zones, mountain shrubs) are not-represented due to their linear shape and small area, and because of the large scale of the maps.

The vector version of program FRAGSTATS (McGarigal and Marks 1995) was used to calculate metrics deemed relevant to sharp-tailed grouse on a landscape scale, including area of each cover type and percentage of landscape composed of the cover type of interest, and the largest patch index (percent of the landscape that the largest patch comprises; McGarigal and Marks 1995). Changes in pattern between historical and current landscapes were described at the cover type level.

Range Expansion Efforts

To determine areas most suitable for habitat improvement given the current vegetation pattern and distribution of core grouse populations, grassland and sagebrush cover types (suitable habitat) were mapped in relation to core populations. Dispersal zones of 20 km from each core population were mapped to determine potential suitable habitat within reach of dispersing juvenile and adult female sharp-tailed grouse. Females were used as a measure of dispersal, because they generally make longer movements than males (Robel et al. 1972, Gratson 1988). The 20-km dispersal distance was used because mean dispersal distance for juvenile female Plains sharp-tailed grouse (*T. p. jamesi*) was 21.6 + 4.0 (SE) km (Robel et al. 1972). In addition, Meints (1991) documented two adult female Columbian sharp-tailed grouse moving 20 km from the lek where they were captured.

Grassland and sagebrush habitats were considered potentially suitable habitat for dispersing grouse, however, patch size must also be considered (Morrison et al. 1992). Home range size was used to determine the minimum patch size which could potentially meet the habitat requirements of an individual. Gratson (1988) found mean fall home ranges for sharp-tailed grouse hens to be 556 ha. Winter home ranges have been reported at 400 ha for males and 251 ha for females (Gratson 1988), 268 ha for sexes combined (Northrup 1991), and 313 ha for males and 177 ha for females (Ulliman 1995). Thus, 556 ha was used as a conservative estimate of sharp-tailed grouse spatial requirements. Grassland and sagebrush patches ≥ 556 ha intersecting 20-km dispersal zones of core populations were used to determine areas most suitable for habitat improvement.

Results

The historical distribution of Columbian sharp-tailed grouse in Washington covered 8,124,201 ha. On the landscape level, patchiness increased from 1,816 patches on the historic landscape to 2,844 patches on the current landscape (Table 1). Consequently, the mean patch size (MPS) decreased by 36%, from 4,474 ha to 2,857 ha.

The largest changes in cover types from the historical landscape to the current landscape occurred in grassland, sagebrush, and cropland/hay/pasture (Table 1). Grasslands diminished from historically occupying 25% of the landscape to 1.3%. The number of grassland patches decreased by 190 (35%), and the largest patch index (LPI) decreased from 17.9% to <0.1%. Furthermore, the grassland MPS decreased from 3,765 ha to 299 ha. The corresponding variability in patch

TABLE 1. Changes from historical (H) to current (C) cover type patterns corresponding with the historical distribution of Columbian sharp-tailed grouse in Washington.

Cover type	CA[1]	%LAND[2]	LPI[3]	NP[4]	MPS[5]	PSSD[6]	PSCV[7]
H-Grassland	2029216	25.0	17.9	539	3765	63025	1675
C-Grassland	104280	1.3	< 0.1	349	299	444	149
H-Sagebrush	3583062	44.1	43.2	267	13420	214113	1596
C-Sagebrush	1264506	15.6	8.3	370	3418	36755	1076
H-Herbaceous wetlands	56313	0.7	0.2	73	7718	2700	3506
C-Herbaceous wetlands	0	0	-	-	-	-	-
H-Wetland shrub	35626	0.4	< 0.1	85	4198	786	1876
C-Wetland shrub	9844	0.1	< 0.1	27	365	560	154
H-Cropland/hay/pasture	0	0	-	-	-	-	-
C-Cropland/hay/pasture	4161861	51.2	38.4	735	5662	115230	2035
Total: Historic	8124201	100	-	1816	4474	-	-
Current	8124201	100	-	2844	2857	-	-

[1] Cover type area (ha)
[2] Percent of landscape (%)
[3] Largest patch index (percent of the landscape that the largest patch comprises; McGarigal and Marks 1995)
[4] Number of patches
[5] Mean patch size (ha)
[6] Patch size standard deviation (ha)
[7] Patch size coefficient of variation (%)

size decreased drastically in both absolute (historical = 63,025 ha, current = 444 ha) and relative (historical = 1,675%, current = 149%) terms.

Sagebrush decreased from being the most prevalent cover type (44.1%) on the historical landscape to occupying only 15.6% of the current landscape. While the number of patches increased through fragmentation from 267 to 370, MPS decreased from 13,420 ha to 3,418 ha. Furthermore, the largest patch decreased from accounting for 43.2% of the landscape to only 8.3% currently (Table 1).

Losses of grassland and sagebrush were due to conversion of these areas to cropland (cropland/hay/pasture). Although cropland was a minor part of the landscape prior to 1900, it currently dominates the southern half of the landscape. The cropland/hay/pasture cover type currently accounts for 51.2% of the landscape and has the highest LPI at 38.4%. In addition, it has the most patches (735) and largest MPS (5,662 ha).

Herbaceous wetlands, which historically covered 56,313 ha, completely disappeared from the landscape, while the wetland shrub cover type diminished by 78% to only 9,844 ha (Table 1). The number of patches of wetland shrub decreased from 85 to 27. These cover types, while only accounting for 1.1% of the historical landscape, may have been very important to sharp-tailed grouse brood-rearing (Gratson 1988, Washington Department of Fish and Wildlife 1995) given their juxtaposition on the landscape (Figure 1).

Range Expansion Efforts

Fifty-seven (16%) of the existing grassland patches occur within or intersect the 20-km dispersal zones surrounding core grouse populations (Figure 2), and six are ≥ 556 ha (median = 751 ha, range = 601 - 1,102 ha) (Table 2). Five of these patches are in the vicinity of the Dyer Hill population, while one is within the Tunk Valley dispersal zone (Figure 2).

Similarly, 37 (10%) of the existing sagebrush patches occur within or intersect the 20-km dispersal zones (Figure 2), and 11 are ≥ 556 ha (median = 4,407 ha, range = 601 - 671,441 ha) (Table 2). The Dyer Hill area accounts for seven patches, Swanson Lakes Wildlife Area for two, Colville Indian Reservation for one, and one patch stretches from Dyer Hill to the Colville Indian Reservation.

TABLE 2. Location and area (ha) of grassland and sagebrush patches ≥ 556 ha intersecting core population dispersal zones of Columbian sharp-tailed grouse in Washington.

Grassland		Sagebrush	
Location	Area	Location	Area
Dyer Hill	1102	Dyer Hill	671441
Dyer Hill	901	Dyer Hill, Reservation	32050
Dyer Hill	801	Swanson Lakes	21733
Dyer Hill	701	Dyer Hill	7712
Dyer Hill	701	Dyer Hill	4607
Tunk Valley	601	Dyer Hill	4407
		Dyer Hill	1202
		Swanson Lakes	1102
		Dyer Hill	1102
		Dyer Hill	901
		Reservation	601

Discussion

The decrease in land area of both grassland and sagebrush, and the increase in patchiness and fragmentation of sagebrush in the study area have resulted from the conversion of native grasslands and sagebrush areas to cropland. These changes and associated agricultural practices, such as plowing stubble, were devastating to the overall population of Columbian sharp-tailed grouse in Washington (Yocom 1952, Buss and Dziedzic 1955).

Grasslands diminished from covering 25% of the landscape to only 1.3%, and grassland MPS decreased from 3,765 to 299 ha. These changes impacted sharp-tailed grouse habitat in two ways. First, total area of the most suitable habitat virtually disappeared. Secondly, the number of patches functioning as quality nesting and brood-rearing habitat for local populations declined drastically. Moreover, the remaining grassland patches might occur in habitat mosaics offering insufficient winter habitat (e.g., riparian areas and mountain shrub patches). For example, the current grassland and sagebrush coverage map (Figure 2) shows that the largest grassland patches occur in the southern part of the historical range, yet no populations exist in these areas. In addition, grouse might be absent from some of these grassland patches due to their position on the landscape (e.g., patch isolation) rather than habitat suitability.

The disappearance of almost all grassland in the Palouse area resulted in the loss of the largest and most contiguous sharp-tailed grouse habitat

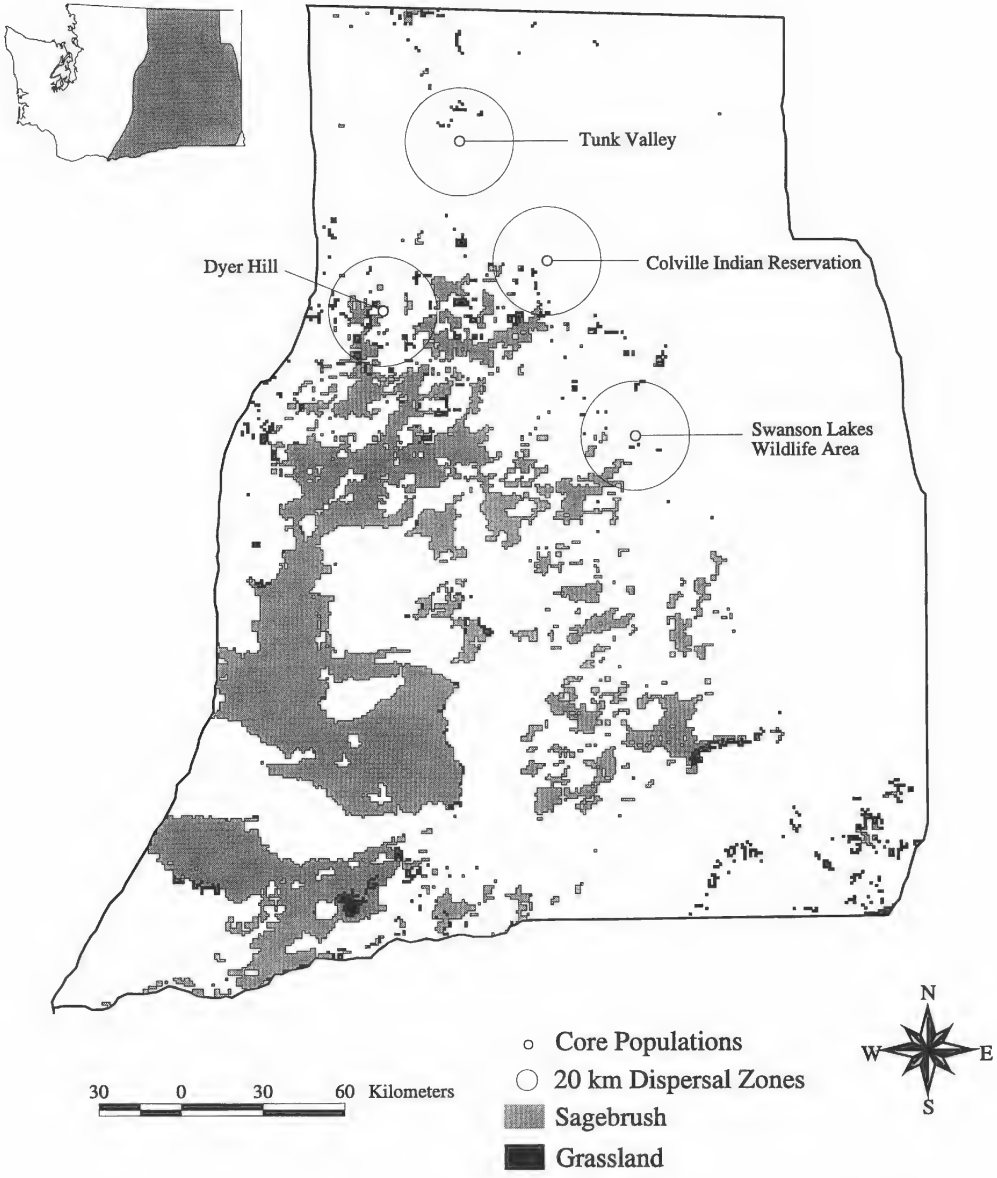


Figure 2. Current (1990) grassland and sagebrush coverage in relation to 20-km dispersal zones for core populations of Columbian sharp-tailed grouse.

within the state (historical LPI = 17.9%). The suitability of this area for sharp-tailed grouse may have been high due to the historical juxtaposition of wetlands within the area (Figure 1). The herbaceous wetlands and wetland shrub cover types occurring in the center of this area most likely offered excellent brood-rearing habitat due to the availability of invertebrates associated with mesic sites. Sharp-tailed grouse broods, similar to other Galliformes, require a diet high in invertebrates during the first few weeks after hatch (Kobriger 1965, Jones 1966).

Sagebrush currently covers 35% of its historical area, and the LPI for sagebrush declined from 43.2% to 8.3%, attesting to the extent of fragmentation. The sagebrush area suffering the greatest fragmentation is in the center of the landscape, adjacent to the Palouse where soils are most productive. This portion of the sagebrush zone may have supported moderate populations of sharp-tailed grouse due to its proximity to the Palouse.

Following the mass conversion and fragmentation of native cover types, distance between suitable habitat patches and landscape resistance to dispersers (decrease in rate of flow of species over a landscape due to structural characteristics) (Forman 1997) have increased, while patch size has decreased. The mean distance from a core grouse population to its nearest neighbor is currently 60.9 km (range = 54.8-71.1 km), triple the mean dispersal distance of females (Robel et al. 1972, Meints 1991), therefore, local population extirpation may likely be permanent. If Columbian sharp-tailed grouse, currently estimated at < 1000 birds in Washington, are to persist, efforts are needed to reconnect remaining core populations through habitat improvement and/or reintroduce grouse into suitable habitats.

Range Expansion Efforts

Habitat improvement and/or reintroduction efforts should be conducted in the vicinity of existing core populations to increase the chances of viable range expansion within Washington. Of the four core populations, the vicinity of the Dyer Hill population has the greatest potential for habitat improvement and range expansion efforts for several reasons. The Dyer Hill population has five of six grassland patches ≥ 556 ha intersecting core population dispersal zones. These five patches are also the largest in size and occur adjacent to relatively large sagebrush patches. Likewise, the majority of sagebrush patches ≥ 556 ha intersecting core population dispersal zones occur in the vicinity of the Dyer Hill population. Because this area has relatively more frequent grassland and sagebrush patches of suitable sizes, it should offer the least landscape resistance to the dispersal and seasonal movements of sharp-tailed grouse.

Efforts should also be made to connect the Dyer Hill population with the Colville population, due to the extent and distribution of grassland and sagebrush patches between the populations. Moreover, the Colville population is the largest of the core populations, and thus may offer the greatest genetic variability and viable source of dispersal.

Riparian zones are one of the most important cover types used during winter, but due to their linear shape and large scale at which the landscape was mapped, are not included in our analysis. These winter habitats need not be large in size, however, they should be distributed throughout the area and juxtaposed to habitats used during the reproductive stage of life (Meints et al. 1992). This habitat mosaic is necessary to meet the seasonal habitat requirements of Columbian sharp-tailed grouse.

A disadvantage to using large scale maps is that some core populations are plotted in the wrong cover type. For example, the Colville population is depicted as occurring in marginal/non-habitat, when it occurs in steppe habitat. While inconsistencies such as this may occur, they should not affect the large-scale changes on the landscape discussed above. However, the results of the grassland and sagebrush coverage intersecting the 20-km dispersal zones of the core populations should be ground-truthed to assess their accuracy and the possibility that suitable patches were not depicted.

Our large-scale analysis provides evidence that appropriate cover types in adequate patch sizes for the recovery of Columbian sharp-tailed grouse populations exist in the study area. Management agencies should determine the quality of these habitat areas and initiate programs to expand the range and promote the conservation of Columbian sharp-tailed grouse in Washington.

Acknowledgments

We thank Liza Fox for her patience, time, and help in the Geographic Information Systems Laboratory, College of Forestry, Wildlife and Range

Sciences, University of Idaho, Stephen Bunting for initial comments on the manuscript, and Michael A. Schroeder for assistance in Washington. This is contribution no. 843 of the University of Idaho College of Forestry, Wildlife and Range Experiment Station.

Literature Cited

Bendire, C. E. 1892. Life histories of North American birds. U.S. Natl. Mus. Spec. Bull. 1.

Buss, I. O., and E. S. Dziedzic. 1955. Relation of cultivation to the disappearance of the Columbian sharp-tailed grouse in southeastern Washington. Condor 57:185-187.

Daubenmire, R. 1988. Steppe vegetation of Washington. Bull. EB 1446, Washington State University Coop. Ext. 131 p.

Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65:169-175.

Forman, R. T. T. 1997. Land mosaics: the ecology of landscapes and regions. Cambridge University Press, Cambridge.

Forman, R. T. T., and M. Godron. 1986. Landscape Ecology. John Wiley & Sons, New York.

Gilpin, M. E., and I. Hanski (eds). 1991. Metapopulation Dynamics: Empirical and Theoretical Investigations. Academic Press, San Diego.

Gratson, M. W. 1988. Spatial patterns, movements, and cover selection by sharp-tailed grouse. Pages 158-192 *in* A. T. Bergerud and M. W. Gratson, eds. Adaptive strategies and population ecology of northern grouse. University Minnesota Press, Minneapolis.

Jewett, S. G., W. P. Taylor, W. T. Shaw, and J. W. Aldrich. 1953. Birds of Washington State. Univ. Washington Press, Seattle.

Jones, R. 1966. Spring, summer and fall foods of the Columbian sharp-tailed grouse in eastern Washington. Condor 68:536-540.

Kobriger, G. D. 1965. Status, movements, habitats, and foods of prairie grouse on a sandhills refuge. J. Wildl. Manage. 29:788-800.

Marks, J. S., and V. S. Marks. 1988. Winter habitat use by Columbian sharp-tailed grouse in western Idaho. J. Wildl. Manage. 52:743-746.

McGarigal, K., and B. J. Marks. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. U.S. Forest Service Gen. Tech. Rep. PNW 351.

Received 30 July 1997
Accepted for publication 3 December 1997

Meints, D. R. 1991. Seasonal movements, habitat use, and productivity of Columbian sharp-tailed grouse in southeastern Idaho. M.S. Thesis, University of Idaho, Moscow.

Meints, D. R. , J. W. Connelly, K. P. Reese, A. R. Sands, and T. P. Hemker. 1992. Habitat suitability index procedures for Columbian sharp-tailed grouse. Id. For., Wildl. and Range Exp. Stn., Bull. 55. University of Idaho. 27 p.

Miller, G. C., and W. D. Graul. 1980. Status of sharp-tailed grouse in North America. Pages 18-28 *in* P. A. Vohs and F. L. Knopf, eds. Proc. Prairie Grouse Symp. Oklahoma State University, Stillwater.

Morrison, M. L., B. G. Marcot, and R. W. Mannan. 1992. Wildlife-habitat relationships: concepts and applications. The University of Wisconsin Press, Madison.

Northrup, R. D. 1991. Sharp-tailed grouse habitat use during fall and winter on The Charles M. Russell National Wildlife Refuge, Montana. M.S. Thesis, Montana State University, Bozeman.

Pickett, S. T. A., and P. S. White (eds). 1985. The Ecology of Natural Disturbances and Patch Dynamics. Academic Press, Orlando.

Quigley, T. M., R. W. Haynes, and R. T. Graham (tech. eds). 1996. Integrated scientific assessment for ecosystem management in the interior Columbia basin and portions of the Klamath and Great Basins. Gen. Tech. Rep. PNW-GTR-382. U. S. Dept. Agric., Forest Service, Pacific Northwest Res. Sta., Portland, OR. 303pp.

Robel, R. J., F. R. Henderson, and W. Jackson. 1972. Some sharp-tailed grouse population statistics from South Dakota. J. Wildl. Manage. 36:87-98.

Ulliman, M. J. 1995. Winter habitat ecology of Columbian sharp-tailed grouse in southeastern Idaho. M.S. Thesis, University of Idaho, Moscow.

Washington Department of Fish and Wildlife. 1995. Washington state management plan for Columbian sharp-tailed grouse. Wildl. Manage. Prog., Wash. Dept. Fish and Wildl., Olympia. 99pp.

Yocom, C. F. 1952. The Columbian sharp-tailed grouse (*Pedioecetes phasianellus columbianus*) in the state of Washington. Am. Midl. Nat. 48:185-192.

Paul H. Whitfield, Environment Canada, 700-1200 West 73rd Avenue, Vancouver, BC, V6P 6H9, Canada

Reporting Scale and the Information Content of Streamflow Data

Abstract

Hydrometric records are collected on a nearly continuous basis in many hydrologic metering programs around the world. These measured signals are typically reported on a time scale longer than the original observations, for instance daily, monthly, or annual runoff. The analysis presented here examined records for several years from a number of watersheds in British Columbia. It addresses whether or not the reporting of daily mean discharge is appropriate for streams of different size scales and from different hydrologic regions of the province. Daily mean discharge is an appropriate reporting scale for watersheds of large area and low precipitation. However in smaller watersheds, and particularly those subjected to coastal rains, a finer time interval is more a more relevant scale.

Introduction

Records of streamflow are collected from networks of stations by many agencies around the world. Caselton and Husain (1980) suggest that the stations in such networks should be considered as transmitting hydrologic information. The hydrologic information is contained in the data records collected manually or automatically. The sampling interval is an important decision in the design of data acquisition systems (Gupta 1973). If there are significant serial correlations, redundant information will result if the sampling is too frequent (Whitfield 1983). However, infrequent sampling would lead to a loss of information (Gupta 1973).

Many gauging programs collect observations continuously and then report data at a time scale much reduced from the scale at which the original measurements were made. One example is that continuous analog records of water levels are converted into daily mean discharges. This daily data contains much information about central tendency, but often much of the hydrologic information contained in the original signal is lost.

Streamflow records have many properties, and many uses. Several authors (Matalas and Langbein 1962; Quimpo and Yang 1970; Gupta 1973) have described the information content of the mean of such records. The information about central tendency contained in such records is used in assessing economic and engineering aspects of water. However, much of the detailed information contained in such records has been lost. Historically, the information which was lost was of little consequence as the amount of detail was difficult, if not impossible, to use in hydrologic analysis. However, several authors have suggested that there be more consideration to time scales in data collection and analysis (Loftis et al. 1991).

Gupta (1973) considered the information content of hydrologic records when reduced from daily values to weekly and monthly records. Gupta (1973) performed a number of analyses considering the information loss which occurs when records were smoothed to means which represent a week or a month.

The present analysis considers this same question when applied to records at a finer time scale; considering the information loss which accompanies the smoothing of records digitized at 15 minute intervals and smoothed to 30 minute, hourly etc. durations. In much of the coastal area of British Columbia, there is considerable detail in records collected at 15 minute intervals (Whitfield and Wade 1992; Wade and Whitfield 1994). The present work considers the information loss that happens when data from a 15 minute sampling interval is smoothed to longer time intervals.

Today, we are increasingly concerned with details, mechanisms, and environmental processes than in the past. Ecosystems operate on a wide range of time and space scales, ranging from fractions of second to thousands of years, and from millimeters to global extent (Steele 1991). Standard methods and standard reporting scales were expedient and efficient for dealing with engineering and economic assessments. However, today we are seeking different types of information from the records, and the availability of hardware and software to process large amounts of data allows us to consider more detailed examination of the records. Specifically we are seeking information

© 1998 by the Northwest Scientific Association. All rights reserved.

about the processes which result in the observed hydrologic events and what the events tell us about the environments and ecosystems.

In the coastal areas of British Columbia rainfall driven streamflow can vary quickly; often very significant changes can occur over a few hours or less. The analysis here relates the information loss to two physical properties of the stations at which the records were collected. First, the examination of information content in relation to drainage area, and second to runoff. It was expected that small watershed with high runoff would have much more complex records, and more information would be lost when records from these stations were smoothed than stations which have large drainage areas and less annual runoff per unit area.

Methods

For each of the cases considered here the primary measurement interval is 15 minutes. These values are the integration of streamflow over 15 minutes rather than discrete samples. Twenty-two hydrometric stations from different hydrologic regions of British Columbia and over a broad range of drainage areas were examined. For each station three separate years of data were assessed. These stations are listed in Table 1 with the drainage area, the long term annual runoff, and the Environment Canada station number. These stations were selected to cover the range of both drainage area and runoff from small to large. A plot of watershed area against runoff in Figure 1 shows the variation amongst the 22 stations studied. These stations were chosen to cover both several orders

TABLE 1. Station number and name for the watersheds with the watershed area and long term annual runoff and the runoff in each of the three years used in this study.

				Mean Annual Discharge in Cubic Meters/second		
	Station	Area (km^2)	Runoff in mms	1991	1992	1993
08HB069	Carnation Creek at 150 m contour	2.53	1576	0.159	0.153	0.143
08HB048	Carnation Creek at the mouth	10.1	2150	0.912	0.740	0.825
08MH098	West Creek near Fort Langley	11.4	704	0.345	0.310	0.261
08NM145	Bulman Creek at the mouth	12.7	176	0.131	0.035	0.089
08MH076	Kanaka Creek near Webster Corners	47.7	1057	2.049	1.640	2.065
08JA016	MacIvor Creek near the mouth	53.4	622	1.744	0.863	1.185
08NK021	Fording River below Clode Creek	104	580	2.955	1.355	2.571
08HC004	Bedwell River above Ursus Creek	114	3258	16.775	12.171	13.425
08NM171	Vaseux Creek above Solco Creek	117	256	1.455	0.607	1.355
08HC002	Ucona River at the mouth	185	2155	15.470	15.552	14.448
08AA009	Giltana Creek near the mouth	194	225	1.772	2.102	1.096
08NE077	Barnes Creek near Needles	201	448	3.571	3.022	3.672
08NG077	St. Mary River below Morris Creek	206	876	6.759	7.734	6.102
08MG001	Chehalis River near Harrison Mills	383	2198	38.435	28.924	28.652
08KA001	Dore River near McBride	404	1365	27.994	21.509	13.393
08JD006	Driftwood River above Kastberg Creek	407	633	11.647	10.807	6.935
08MF068	Coquihalla River above Alexander Creek	720	1113	39.564	25.507	26.377
08KH010	Horsefly River above McKinley Creek	785	772	22.351	21.351	25.415
08NM116	Mission Creek near East Kelowna	811	232	9.096	3.644	8.750
08GA022	Squamish River near Brackendale	2330	2575	256.929	252.589	175.033
08GD004	Homathko River at the mouth	5720	1581	396.308	333.401	301.609
08MF005	Fraser River at Hope	217000	343	3100.473	2931.958	2468.117

of magnitude in drainage area and from low runoff to high runoff watersheds.

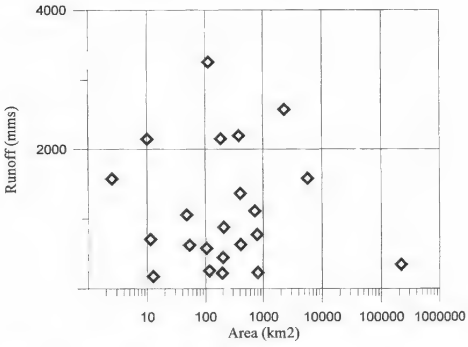


Figure 1. Runoff and drainage area relationships for the 22 hydrologic stations described in Table 1.

Each series was smoothed from 15 minute observations to 30 minute averages, 1 hour averages, 2 hour, 4 hour, 8 hour, 1 day and 2 day averages. Each of these smoothed series has the same mean as the initial series. The autocorrelation function of each of these series was calculated. One problem with the interpretation of the lag one autocorrelation is the differences in the degrees of freedom between the 15 minute data and the smoothed versions. When smoothed to one day there is approximately a loss of 100 degrees of freedom. While the total degrees of freedom for all cases is large, it is not equal between the various curves.

The assessments of information loss was based on the assessment of two properties of the original and smoothed records. The first of these is the autocorrelation of the values in the time series. The autocorrelation is a measure of the relationship between each observation and the next one in the series and is calculated using:

$$r_k = \frac{\sum(x_t - \bar{x})(x_{t+k} - \bar{x})}{\sum(x_t - \bar{x})^2}$$

where x_t is an observation at time t, and $\bar{x}$ is the mean of the series. When values in the sequence are similar the autocorrelation value will approach a value of one. If the series is random, the value will approach zero.

The second property is a measure of the amount of information contained in the variance of the values in the series compared to the total variance of the entire data set. While several estimators of the information content have been proposed von Neumann's variance ratio was chosen (von Neumann et al.; 1941; von Neumann 1941). The Von-Neumann's variance ratio was calculated using:

$$\frac{\sigma^2}{S^2} = \frac{\sum(x_t - x_{t-1})^2 / (T - 1)}{\sum(x_t - \bar{x})^2 / T}$$

Where x_t is an observation at time t, $\bar{x}$ is the mean of the series and T is the total number of observations. Von-Neumann's ratio is essentially the ratio of the variance of the points in the series, one to the next, against the statistical variance of the entire series. This provides a measure of the information content of the series of observations, and as it approaches unity indicates that the point to point variance approaches the statistical variance. An important feature of Von-Neumann's variance ratio is that the effect of sample sizes associated with the smoothing of the raw data is removed (von Neumann 1941).

Results

The difference between 15 minutes accumulations and daily mean discharges are shown in Figure 2. A sixteen day interval is shown for a small watershed (Figure 2a) and for the same period in a large watershed (Figure 2b). These are typical examples of the impact of smoothing. For Carnation Creek, a small high discharge stream, the impact of the smoothing is quite obvious (Figure 2a). Here the observed streamflow is only grossly represented by the daily mean discharge. For the Fraser River at Hope, a large river with a large drainage area, the daily mean streamflow more closely represents the original observations (Figure 2b). In particular, the smoothing which takes place for a large river results in the expected integration, however, for the smaller coastal stream there is a complete obliteration of the signal. This then demonstrates that the records of the daily mean discharges significantly alters the information content of the original measurements.

Sampling Rate

Estimates of the lag 1 autocorrelation coefficient and the Von-Neumann's variance ratio were obtained for each of the 22 rivers and streams, for

three separate years (1991, 1992, and 1993). The results for each of the three years were similar, and the average lag 1 autocorrelation for the three years for each stream and each level of smoothing is presented in Figure 3. For all streams, the autocorrelation coefficient increases with the

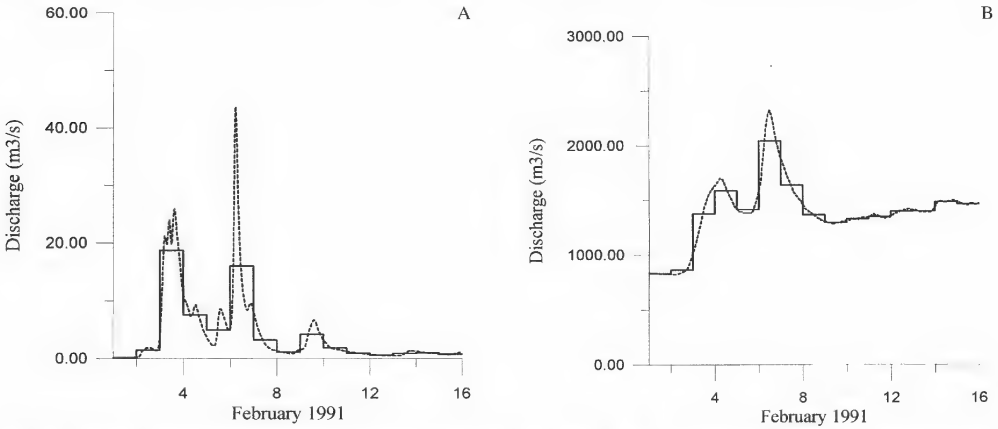


Figure 2. Streamflow records as measured and as reported for a six day period for a high runoff small watershed A and for a large drainage basin B. The dashed line is the series of 15 minute measurements and the solid line is the reported daily value.

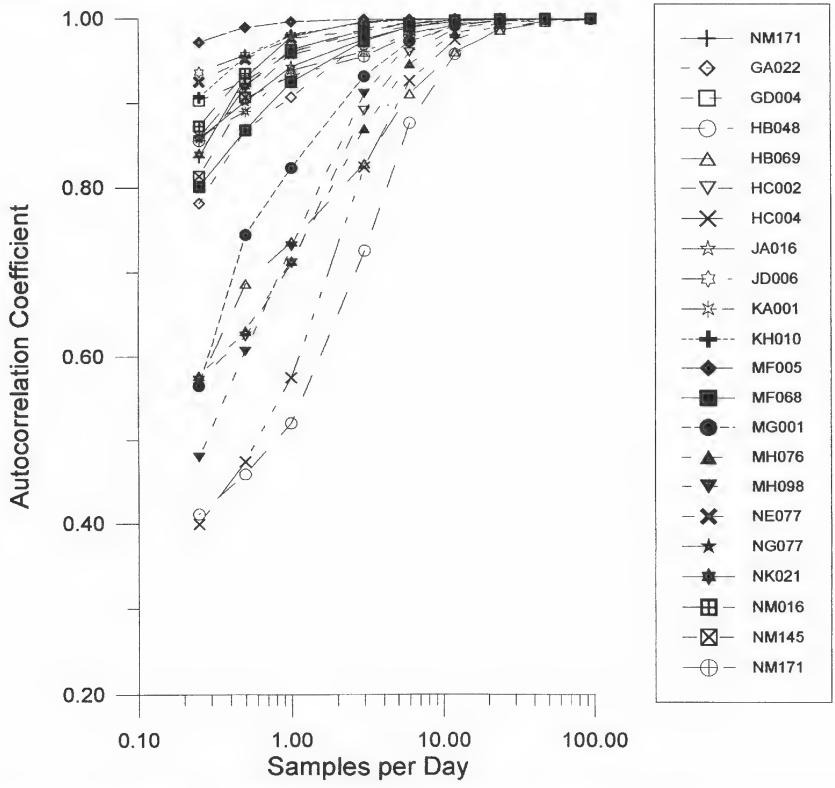


Figure 3. Mean lag 1 autocorrelation coefficient as a function of reporting interval for the 22 hydrologic stations.

number of samples reported per day, indicating that as the density of samples increases the time series which are generated contain less independence between measurements. In larger streams, such as the Fraser River at Hope [MF005] the lag 1 autocorrelation remains near unity until the reporting interval is multiple days. Small coastal streams such as Carnation Creek at the Mouth [HB048] and Bedwell River [HC004] have very low lag 1 autocorrelations when the number of samples reported per day is reduced. In particular, consider the range of observed autocorrelations at the reporting interval of one per day. The lag 1 autocorrelation coefficient varies from 0.5 to nearly 1. This result alone suggests that the information content of such records is different, and the amount of redundant information contained in those records is also different.

There is a relationship between the reporting frequency and the von Neumann's variance ratio for all streams. As the number of samples reported per day increase there is a reduction of the ratio (Figure 4). This reduction in the ratio is in total several orders of magnitude. For all rivers there is a substantial difference between almost every sampling interval. In effect, as the reporting frequency increases there is more information about the signal captured. Considering the reporting interval of one day, there is more than a two order of magnitude variation [1.0 to less that .01] across the stations considered. When the ratio is less than unity the point to point variance in

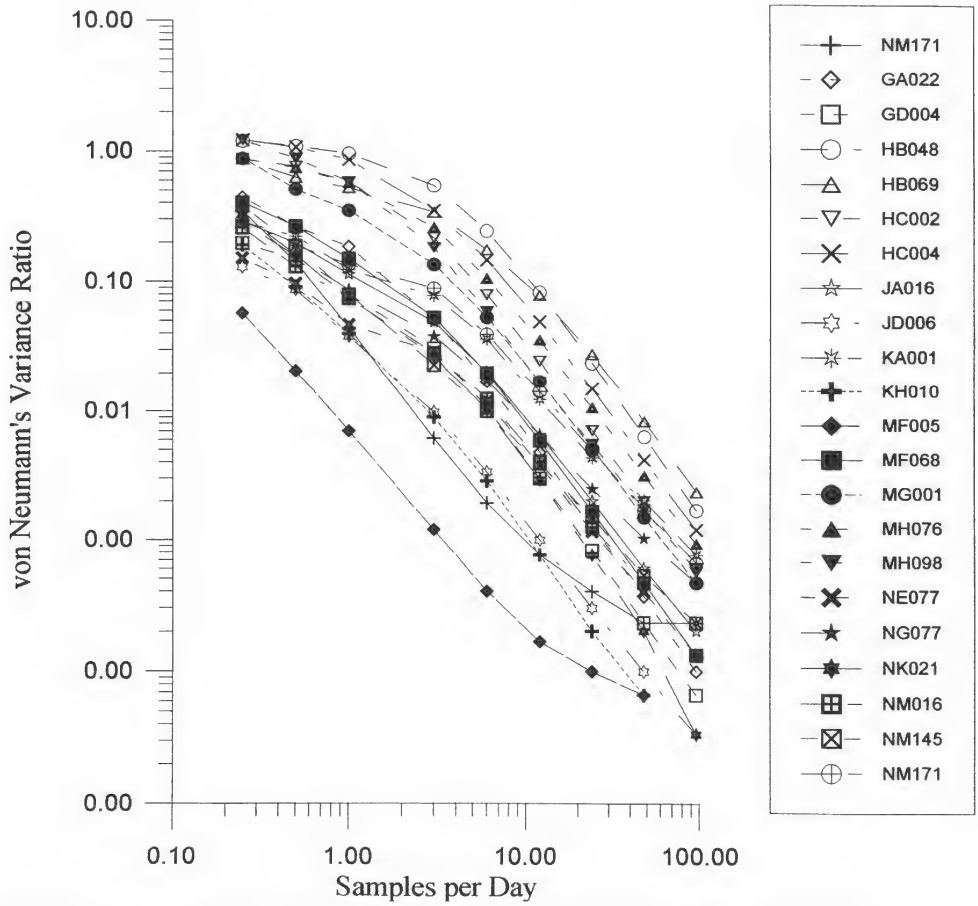


Figure 4. Mean von Neumann's variance ratio as a function of reporting interval for the 22 hydrologic stations.

the series is less than the total variance, indicating that there is significant serial correlation between successive points. As the statistic increases towards unity there is less serial correlation in the data. Thus, for one reporting frequency (i.e. one per day) there is a substantial difference between this statistic across the 22 streams considered.

On the other hand, consider that it might be desirable to hold this statistic constant for all streams in a network, in a case where the same level of information about each station was needed. Consider that a Von-Neumann's variance ratio of 0.01 was important for providing adequate hydrologic data. In such as case, some river could be reported once per day (Fraser River at Hope [MF005]) while others would require more frequent reporting (e.g. Carnation Creek [HB069] ~50 times per day).

Drainage Area

In the preceding results it was suggested that smaller watershed have a more complex hydrologic record, and that more frequent reporting provides more information. A plot of drainage area against lag 1 autocorrelation coefficient (Figure 5) shows that there is a tendency for low lag 1 autocorrelations to be associated with small

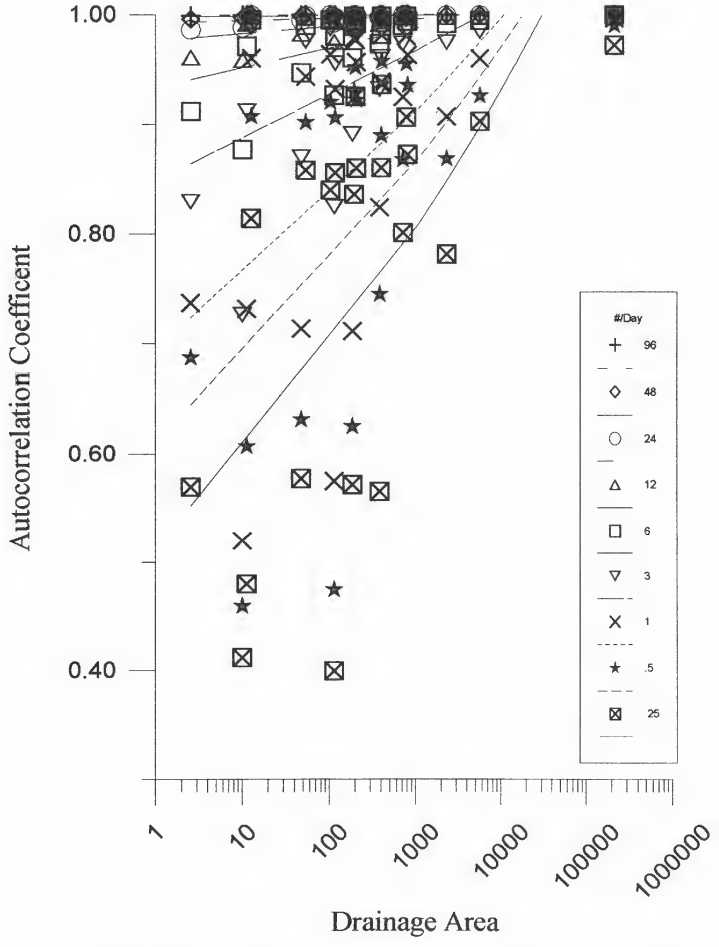


Figure 5. Mean lag 1 autocorrelation coefficient as a function of drainage area for the nine reporting intervals for the 22 hydrologic stations.

drainage basins. This is not a consistent trend, as there are basins of similar area which have very different coefficients for a sampling frequency, yet have similar areas. This is best illustrated by considering one of the lower reporting frequencies. At one sample per day, for example, there the coefficient is high [>0.9] at the largest drainage areas [10000 km^2] but much more variable in smaller drainage basins, ranging from 0.5 to >0.9.

A much clearer pattern exists for the relationship of Von-Neumann's variance ratio to drainage area. There is a consistent decrease in the ratio across the various reporting intervals for the range of drainage areas considered here (Figure 6). This decrease is about one order of magnitude for each of the reporting frequencies from the smallest watershed to the largest.

Runoff

The other hydrologic variable which was considered to be important was runoff. The lag 1 autocorrelation decreased with increasing runoff (Figure 7) particularly for highly smoothed data (0.25). This suggests that there is less correlation

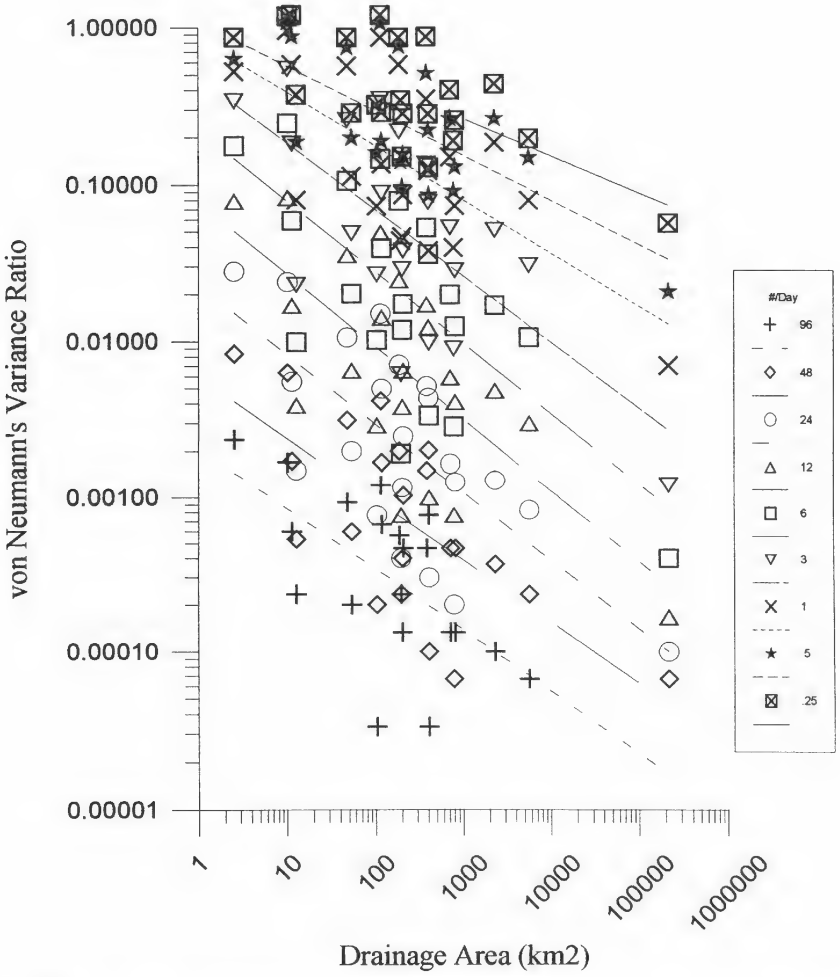


Figure 6. Mean von Neumann's variance ratio as a function of drainage area for the nine reporting intervals for the 22 hydrologic stations.

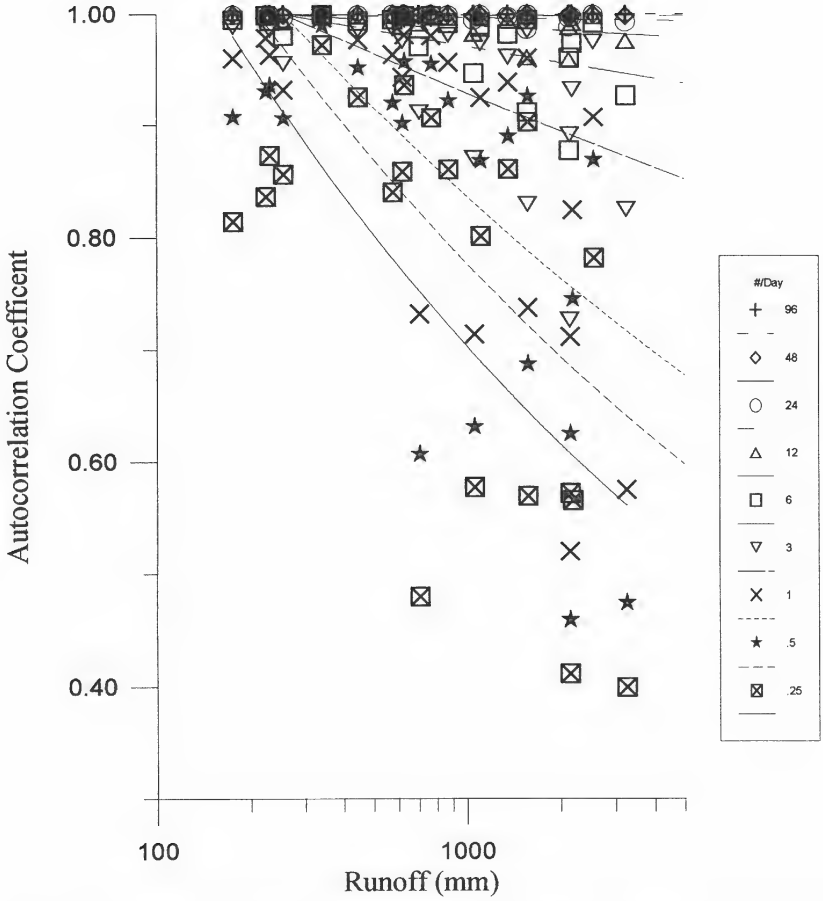


Figure 7. Mean lag 1 autocorrelation coefficient as a function of runoff for the nine reporting intervals for the 22 hydrologic stations.

amongst values in a series from a high runoff stream which has been highly smoothed. There is significant scatter between coefficients for stations of similar area despite the general trend. For the highest reporting frequencies, the autocorrelation for lag one are near unity.

Von-Neumann's variance ratio results have a relationship to runoff. Von-Neumann's ratio increases with increasing runoff for any reporting interval (Figure 8). Generally, there is about one order of magnitude increase in the ratio between the lowest runoff watershed and the highest; however there is considerable scatter about the relationship. This result reflects the higher complexity of the signal in higher runoff streams.

Discussion

The choice of sampling interval is an important decision in the design of data acquisition systems (Gupta 1973; Loftis et al. 1991). The final decision regarding the interval is a compromise between maximizing the information content of the signal and minimizing the collection and storage of redundant information. One possible approach is a sampling interval which minimizes variance and thus maximizes the information content (Gupta 1973). To achieve this Gupta suggests setting a threshold based on information content which balances the information content of the signal against the collection of redundant information. In his study he used a threshold of 0.80 for two

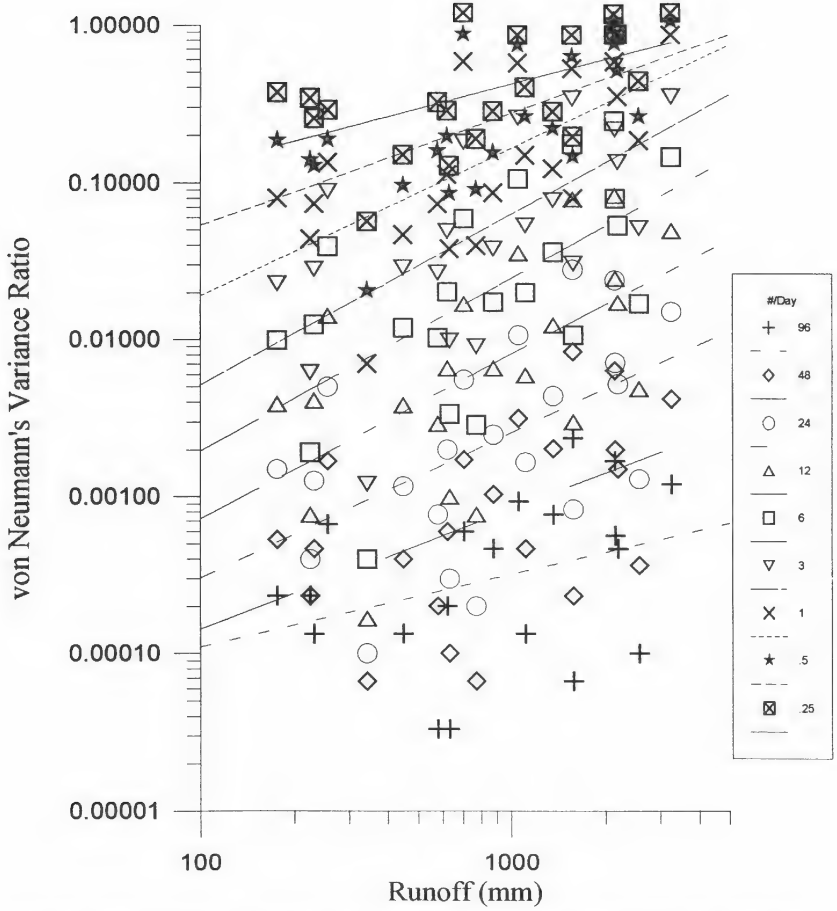


Figure 8. Mean von Neumann's variance ratio as a function of runoff for the nine reporting intervals for the 22 hydrologic stations.

water years from three sites in watersheds with areas of about 100 km^2. In addition Gupta actually resampled the record at discrete intervals—a record which had been created by accumulation and averaging to daily mean flows.

The results presented here show that selecting one size watershed from one geographic region could be misleading. The information content of streamflow records is related to both the runoff and the area of the watershed. The correlation function is a measure of the reservoir mechanism in the watershed (Glottschalk 1977). Caselton and Husain (1980) suggest that there should be a scientific basis for the design and operation of hydrologic networks. One of the important decisions which must be made when developing a network is how the results will be reported. The results here suggest that reporting on one time interval results in a significant loss of detail contained in the original signal. While this information loss may be small in terms of central tendency measures, these details are important in other types of analysis. High frequency water quality monitoring has revealed information about processes taking place within the ecosystem (Whitfield and Wade 1992; Wade and Whitfield 1994). As the interest in ecosystems increases the focus is shifting from means and variances to detailed analysis of processes.

From this analysis it appears that both watershed area and runoff have a strong influence on the information content of hydrologic records. These difference indicated that the response characteristics of watersheds vary with both size and with runoff. This may be considered as a property related to the residence time of water within the watershed. Small watersheds with high runoff have highly variable hydrographs. The information content of records is reduced and the signal obliterated when reported on a time interval greater than the scale at which events take place in that watershed. The information content of such records is not equal across a broad range of drainage areas, nor across a range of annual runoffs.

Conclusions

The information content of records is a useful perspective to consider when designing the collection of a hydrologic record (Gupta 1973). Caselton and Husain (1980) suggest that information content is an important criteria to consider when developing the scientific basis for network operation. The present results support this observation and demonstrate the loss of information which results from operating in a single reporting scale.

Acknowledgments

The author would like to express his appreciation to Lynn Campo and the Water Survey of Canada staff who produced the data on which this study is based, and to Dr. Rory Leith for the contribution of his comments and suggestions to this work.

Literature Cited

Caselton, W. F. and T. Husain. 1980. Hydrologic Networks: Information Content. J. Water Resources Planning and Management Division ASCE 106:503-520.

Glottschalk, L. 1977. Correlation structure and time scale of simple hydrologic systems. Nordic Hydrology 8:129-140.

Gupta, V. L. 1973. Information Content of Time-variant data. J. Hydraulics Div. ASCE 99:383-394.

Loftis, J. C., G. B. McBride, and J.C. Ellis. 1991. Considerations of scale in water quality monitoring and data analysis. Water Resources Bulletin 27:255-264.

Matalas, N. C., and W. B. Langbein. 1962. Information content of the mean. J. Geophysical Research 67:3441-3448.

Quimpo, R. G. and J. Y. Yang. 1970. Sampling considerations in stream discharge and temperature. Water Resources Research 6:1771-1774.

Received 30 July 1997
Accepted for publication 13 November 1997

Steele, J. H., 1991. Marine ecosystem dynamics: comparison of scales. Ecological Research 6:175-183.

von Neumann, J. 1941. Distribution of the ratio of mean square successive difference to the variance. Annals of Mathematical Statistics 12:367-395.

von Neumann, J., R. H. Kent, H. R. Bellenson, and B. I. Hart. 1941. The mean square successive difference. Annals of Mathematical Statistics 12:153-162.

Wade, N. L., and P. H. Whitfield. 1994. Observing transient water quality events using electronic sensors. In: National Symposium on Water Quality. American Water Resources Association. pp 105-112.

Whitfield, P. H., 1983. Evaluation of water quality sampling locations on the Yukon River. Water Resources Bulletin 19:115-121.

Whitfield, P. H., and N. L. Wade. 1992. Monitoring transient water quality events electronically. Water Resources Bulletin 28:703-711.

Northwest Science Forum

Northwest Science Forum provides an opportunity to articulate and discuss scientific issues in a less structured format than peer-reviewed articles. The Forum publishes short articles, opinion pieces, and letters with a focus on science and natural resource issues in the Pacific Northwest. Although the Forum is not peer-reviewed, it is edited for format and clarity. Articles should generally be less than 2000 words and contain minimal literature citations. Letters in response to articles are particularly encouraged; the original author will normally be given a chance to respond to the letter as well. There are no page charges or reprints associated with the Forum, and participants need not be members of the Northwest Scientific Association. Please send all submissions, including two hard copies and an electronic copy (any recent version of Word or WordPerfect) to the Editor.

Debra J. Salazar with **Nicole Oliver,**[1] Department of Political Science, Western Washington University, Bellingham, Washington 98225-9082

Environmental Justice and Natural Resource Management in the Pacific Northwest

The relation between natural resource management and environmental justice may not be immediately apparent to those engaged in natural resource science and management in the Pacific Northwest. For many, environmental justice calls to mind struggles over exposure to toxic substances. Indeed proponents of environmental justice argue that poor and dark-skinned peoples throughout the world are disproportionately exposed to environmental toxins (Bryant and Mohai 1992; Bullard 1990, 1993). In response to these threats to their health, many communities have mobilized to fight the construction of hazardous facilities in their neighborhoods, to compel emissions reductions from existing facilities, or to be compensated for damages suffered as a result of exposure to hazardous substances. Love Canal in New York is the most prominent example, but similar efforts were undertaken in Woburn, Massachusetts; Houston, Texas; and Kettleman City, California, to name just a few places. During the last decade such battles have become increasingly common.

But the struggle for environmental justice entails more than fighting against exposure to toxins. A comprehensive conception of environmental justice must take account of environmental *goods* (e.g., wildlife habitat, high quality wood, wild salmon) as well as *bads* (pollutants). That is, environmental justice encompasses resource management issues as well as pollution problems. Thus natural resource managers and scientists ought to be concerned with environmental justice. Moreover, focusing on three elements of environmental justice will highlight implications for resource management and science in the Pacific Northwest.

Social Justice and Resource Management

Twenty-two years ago I was a forestry student at the University of California. One fall afternoon on a field trip in the Berkeley hills we were standing in an open, oak-bay woodland with knobcone pine

[1]Debra Salazar is Professor of Political Science and Affiliate Professor of Environmental Studies at Western Washington University. Nicole Oliver is an M.A. candidate in Political Science at Western Washington University. This paper is a revised version of a lecture Salazar presented at the University of Vermont, School of Natural Resources, September, 1997. The authors thank Aundrea Noffke and Lisa Moulds for their comments.

and coast redwood in the draws on the opposite slope. It was an inspiring landscape and nearly all of us were pleased that our choices to date had allowed us time there. One of my classmates asked the professor how we might define good management of this landscape. The professor replied that there was no such thing as good resource management in the abstract. Good management was management that met the objectives of the owner. As foresters, our job would be to manipulate the landscape in the service of those objectives. I was intrigued by this notion at the time, struggled with it, but never really accepted it.

Presumably those of us who study natural resources, do so out of interest and because we care about resources, landscapes, the earth. Like my classmate twenty-two years ago, we are committed to good management and we have some ideas about how to assess what is good. These ideas can range from the abstract (sustainability) to the concrete (cost-effective wood production or protection of endangered species). I am suggesting here that our commitment ought to extend to people, especially the least powerful people.

Resource management is political—that is, particular management strategies favor some people and disfavor others. Each resource management decision implies a choice about what is fair in a particular context. Resource managers can make such decisions without explicit consideration of fairness. Alternatively they can promote equal access to natural resources and attempt to ensure that the least powerful receive a fair share of the benefits of resource management. The latter approach will lead to a more just society and this is an appropriate goal of resource management.

Elements of Environmental Justice

Only during the last decade and a half have social scientists attempted to test the proposition that environmental bads are unfairly distributed. Early research found that dark-skinned and/or poor people were more likely to live in poisonous environments than those who are light-skinned and affluent (US General Accounting Office 1983; United Church of Christ 1987; Bullard 1990; Bryant and Mohai 1992). More recent studies have reached conflicting conclusions (e.g., Oakes *et al.* 1996; Pulido 1996; Pollock and Vittas 1995; Hamilton 1995; Anderton *et al.* 1994). But the bulk of the evidence suggests that one's political economic status is a key determinant of the quality of one's environment. For example, black children have a higher probability of dangerous levels of lead in their blood than do white children (Centers for Disease Control, 1988). Such children, often living in dilapidated housing, have no effective representation. Their parents lack political power and thus are excluded from decision-making arenas that could address the problem of lead paint exposure. Similarly farmworkers, exempt from most labor legislation, have waged a long and frustrating campaign to protect themselves and their families from the deleterious effects of agricultural pesticides. Epidemiological studies of farmworkers and their children reveal elevated rates of skin diseases, several types of cancer, spontaneous abortions, and several kinds of birth defects as well as other conditions (Moses 1993). But despite years of effort, farmworkers have had little success in their effort to limit their exposure to agricultural pesticides.

These examples suggest opportunities for environmental policy actors to take the initiative in improving the environments of marginalized people. Similarly, natural resource policies and practices offer an opportunity to mitigate, or to reinforce, social inequity. If resource management proceeds without attention to environmental injustice, the latter is more likely to occur.

Applying the concept of environmental justice to resource management suggests three defining elements (Salazar 1996). The first requisite of environmental justice is that natural resources be allocated through fair procedures. Allocation refers to decisions about *how resources will be used.* Second, the benefits and costs of resource management should be distributed fairly. Third, citizens should have equal access to public resources. Examination of each of these elements will highlight the relation between resource management and environmental justice.

Fair Procedures for Resource Sllocation

The central issue in most natural resource policy debates is allocation. Shall our forests serve as wildlife habitat, as tree farms, or as the setting for suburban subdivisions? The issue of distribution, who will reap the benefits and bear the costs of resource use, often is not addressed.

Although allocation and distribution are analytically distinct, they are not so in practice. The distribution of wealth in society will affect the resource allocations that occur; the most affluent are likely to exercise disproportionate influence in determining how our forests are used. Similarly, resource allocations may have distributive consequences; restricting the harvest of firewood in national forests may decrease the standard of living available to working class, rural residents. If resource allocation decisions are to produce just results, they must attend to the voices and interests of all relevant segments of society, including the least powerful.

Of course designing decision-making procedures that achieve this end is not simple. A strategy increasingly used to facilitate open discussion and accommodation of conflicting interests is multi-stakeholder, consensus processes. But even these processes may perpetuate inequities. In 1992 the premier of British Columbia created the Commission on Resources and Environment (CORE) to oversee regional planning for land use allocation. CORE was established in response to escalating conflict between environmentalists and logging interests, as well as a growing public perception that BC's forests were mismanaged (Salazar and Alper 1997). The goal of CORE was to bring together all relevant interests in a mediated, consensus negotiation (Burrows, 1997).

The CORE process failed both to achieve consensus among the participants and to generate a land use allocation that had broad public support (Burrows 1997; Salazar and Alper 1996). Moreover, the CORE process reinforced existing social inequities. Participation in CORE required stakeholders to invest hundreds of hours of volunteer time to attend nearly a year of 2-3 day, monthly meetings. The structure of CORE pitted paid, professional representatives of timber, mining, agriculture and forest employment interests against volunteer representatives of environmental and community organizations. These less affluent sectors lacked the time, access to technical information, and negotiating expertise that was available to wealthier participants.

The CORE example highlights several issues that are implicit in the structure of resource allocation procedures. What are appropriate criteria for selecting participants? Should they be citizens? Such a requirement would exclude participation of multi-national corporations. But should such corporations participate with the same status as citizens? How can broad public interests be addressed? How can participation by less affluent sectors be facilitated? A fair procedure does not imply a single answer to any of these questions. Rather, by raising the questions, and attempting to answer them in a public arena, where the answers must be defended, policy makers and managers move closer to environmentally just resource management.

Fair Distribution of the Benefits and Costs of Resource Management

Fair distribution is the second requisite of environmental justice. The public park provides a good illustration of the operation of this criterion. In the United States, all levels of government operate park systems. But the federal government plays a key role in providing funding for state and local, as well as national parks (National Academy of Sciences 1993). Every year Congress appropriates millions of dollars from the Land and Water Conservation Fund (LWCF) for federal projects, and awards matching grants for state park and recreation projects. Created in 1964, the Fund's initial purpose was to finance land purchases to provide public outdoor recreation opportunities. Subsequent amendments and a changing definition of conservation have allowed the Fund to be accessed for wildlife refuges and protection of habitat for endangered species. The National Park Service, the primary federal beneficiary of the Fund, determines which projects have priority and which interests will benefit from LWCF expenditures. Judgments about fairness are implicit in these allocations. They imply an assessment of the relative priority of recreation land accessible to urban areas versus biodiversity protection through preservation of large, wild areas. How can the Fund be managed to achieve both of these social goals? Under what conditions should one have priority over the other?

Management and allocation of open space in urban areas also raises issues of environmental justice. How are parks distributed across neighborhoods in Portland and Seattle? Do residents of northeast Portland and the Rainier Valley of Seattle have access to the same quality of parks as residents of the wealthier neighborhoods of these cities? On a smaller scale than parks, consider

street trees. Are they distributed evenly in cities? Nature in the city is highly valued and available to those willing and able to pay for it. How can our public policies ensure that all people will have access to a nature that can enrich their lives?

While the preceding examples focus on the benefits of resource management (access to outdoor recreation opportunities), natural resource policies also create costs. In the Northwest, many of those employed in the resource extraction industries, while having benefited from management policies in the past, now suffer financial and other kinds of losses as a result of these policies. The long term trend of industrialization of wood and fish harvesting and processing, and the recent implementation of environmental protection in both sectors have contributed to economic decline for many workers. Resource analysts can attempt to assess the fairness of the distribution of losses as well as to find ways to minimize them. Once again, attention to environmental justice does not provide answers. Instead it focuses attention on a set of questions.

Equal Access to Public Resources

Ensuring equal access to public resources requires that policy makers determine which resources are public, identify relevant publics, and devise means to secure equal access. Failure to resolve these issues continues to hinder efforts to conserve wild salmon. While fish and wildlife long have been considered public resources, only during the last three decades have public policies attempted to protect habitat. Forest practice, wetlands, and land use laws, have met with considerable resistance from many land owners (Switzer 1997). They have argued that there is no public right to their land and that they should be compensated for any restrictions on land use. Proponents of regulatory laws argue that the habitat requirements of fish and wildlife necessitate some public control over private land. These contending positions on property rights reflect different conceptions of what is fair or just. We will not reach consensus on the appropriate extent of public authority regarding habitat protection but resource managers and scientists can draw on their expertise to contribute to policy discussion.

This discussion should be open to all relevant actors, but groups without political influence often have had to resort to the courts to secure their inclusion. Native American tribes fought a long battle to assert their treaty rights to participate in the development of policies and practices that affect salmon populations. Now their treaty rights are acknowledged to include both habitat protection and an equal share of the harvest. But conflict between tribal and non-tribal fishers remains an impediment to the development of policies that would serve the long-term interests of both groups. Securing meaningful access to a resource often requires managing conflict between competing user groups. This is an undertaking to which both resource managers and scientists can contribute.

Natural Resource Science and Environmental Justice

Attention to environmental justice surely makes resource management more complex. It raises many questions and answers few. But consideration of environmental justice does more than complicate resource management. It also suggests avenues for applied research, research that might contribute to more just and sustainable resource policies and practices. For example, we are only beginning to recognize the extent and value of the forest floor economy (Brown 1997; Emery 1997; Richards and Creasy 1996). Harvest of forest floor products (e.g., berries, mushrooms, boughs, leaves, cones) increasingly supplies not only subsistence but the basis for a dynamic cash economy. Yet we know little about this economy or its ecological and social implications. Scientists with a commitment to environmental justice are more likely to be aware of the often marginal participants (many are poor, immigrant, non-English speaking) in the forest floor economy. These scientists are positioned to extend their research programs, addressing the social and biological questions raised by harvest of non-timber forest products. Such research might contribute to the sustainability of the forest floor economy and to improved working conditions for the non-timber labor force.

A commitment to environmentally just resource management does not require that scientists or managers become advocates for particular interests or resource allocations. Rather such a commitment obliges us to ensure that difficult questions are raised and addressed. Not all will be suited to this role; but for those who can manage this expansion of their professional agenda, it is an appropriate and necessary role.

Lterature Cited

Anderton, Douglas L., Andy B. Anderson, John M. Oakes, and Michael R. Fraser. 1994. Environmental Equity: The Demographics of Dumping. *Demography*:31(2):229-248.

Brown, Beverly A. 1997. The Multi-Ethnic, Non-Timber Forest Workforce in the Pacific Northwest: Reconceiving the Players in Forest Management. Unpublished paper presented at Sustaining the Forests of the Pacific Coast: Nature, Politics, and Markets (lecture series), Western Washington University, Bellingham, Washington.

Bryant, Bunyan and Paul Mohai. 1992. *Race and the Incidence of Environmental Hazards: A Time for Discourse.* Boulder, CO: Westview Press.

Bullard, Robert D. 1990. *Dumping in Dixie: Race, Class and Environmental Quality.* Boulder, CO: Westview Press.

Bullard, Robert D. 1993. *Confronting Environmental Racism: Voices from the Grassroots.* Boston: South End Press.

Burrows, Mae. 1997. Multi-Stakeholder Processes: Activist Containment vs. Grassroots Mobilization. Unpublished paper presented at Sustaining the Pacific Coast Forests: Nature, Politics, and Markets (lecture series), Western Washington University, Bellingham, Washington.

Centers for Disease Control. 1988. *The Nature and Extent of Lead Poisoning in Children in the United States: A Report to Congress.* Atlanta: Centers for Disease Control, Substances and Disease Registry.

Emery, Marla. 1997. Rainforest Crunch From Michigan? Non-Timber Forest Products & Household Livelihoods In a Northern Latitude. Paper presented at annual meeting of Association of American Geographers.

Hamilton, James T. 1995. Testing for Environmental Racism: Prejudice, Profits, Political Power? *Journal of Policy Analysis and Management* 14(1):107-132.

Moses, Marion. 1993. Farmworkers and Pesticides. In Robert D. Bullard, *Confronting Environmental Racism: Voices from the Grassroots.* Boston: South End Press. 161-78

National Academy of Sciences. 1993. Setting Priorities for Land Conservation. Washington, DC: National Academy Press.

Oakes, John M., Douglas L. Anderton and Andy B. Anderson. 1996. A Longitudinal Analysis of Environmental Equity in Communities with Hazardous Waste Facilities. *Social Science Research* 25(2):125-148.

Pollock, Philip H. III and M. Eliot Vittas. 1995. Who Bears the Burdens of Environmental Pollution? Race, Ethnicity, and Environmental Equity in Florida. *Social Science Quarterly* 76(2):294-310.

Pulido, Laura. 1996. *Environmentalism and Economic Justice: Two Chicano Struggles in the Southwest.* Tucson: University of Arizona Press.

Richards, Rebecca T. and Max Creasy. 1996. Ethnic Diversity, Resource Values, and Ecosystem Management: Matsutake Mushroom Harvesting in the Klamath Bioregion. *Society and Natural Resources* 9(4):359-374.

Salazar, Debra J. 1996. Environmental Justice and a People's Forestry. *Journal of Forestry* 94(11):32-36.

Salazar, Debra J. and Donald K. Alper. 1996. Perceptions of Power and the Management of Environmental Conflict: Forest Politics in British Columbia. *Social Science Journal* 33(4):381-399.

Switzer, Jacqueline Vaughn. 1997. *Green Backlash: The History and Politics of Environmental Opposition in the US.* Boulder: Lynne Rienner Publishers.

United Church of Christ. 1987. *Toxic Wastes and Race in the United States: A National Report on the Racial and Socio-Economic Characteristics of Communities with Hazardous Waste Sites.* New York: United Church of Christ, Commission for Racial Justice.

U.S. General Accounting Office. 1983. *Siting of Hazardous Waste Landfills and Their Correlation with Racial and Economic Status of Surrounding Communities.* Washington, DC: US General Accounting Office.

Book Reviews

Geographic Variation in Forest Trees: Genetic Basis and Application of Knowledge in Silviculture

E. Kristian Morgenstern, 1996, UBC Press ($39.95)

Just as natural resource managers should look at the landscape when making management decisions, they should not neglect the genetic level. The genetic variations inherent in tree populations impact how forest landscapes develop. These variations are dynamic, responding to environmental changes, adapting individual trees to create a population structure of provenances across the range of a given species. Failure to recognize these variations can lead to plantation failures and temporal setbacks in harvest schedules. Complete disregard for the importance of natural genetic variations could result in catastrophic affects on genetically improved seedlings commonly planted around the world today. Dr. Kristian Morgenstern has written a book that draws the natural resource manager's attention to this genetic variation and its relevance to silvicultural applications.

Chapter one introduces the reader to the history of genetic research. This historical background focuses on three areas: plant breeding research between the years 1700 and 1900; the development of quantitative methods to assess genetic theories; and, the establishment of methods and programs to test for genetic processes beyond natural selection and mutation. Dr. Morgenstern presents developments in these three areas in chronological order, highlighting, where literature is available, progress associated with forest tree species.

In Chapter two, Dr. Morgenstern provides the reader with a succinct review of population genetics. Here one finds definitions, concepts and theories that underlie the study of genetic variation. The review is presented in two sections, one on genetic processes and one on genetic systems. In this chapter, Dr. Morgenstern gives background critical to understanding the concepts presented in chapters three, four and five.

Chapters three and four bring the natural resource manager into familiar territory, but from the genetic perspective. The impact of environmental factors and geographic variation on intraspecies differentiation is reviewed. While differences in phenotypes may not be new to some readers, Dr. Morgenstern's writings provide an understanding of how phenotypic characteristics arise as a result of interactions between environmental factors and genetic systems. From variations arising from geological and climatic changes, to clinal differences associated with elevation and latitude, the reader is left with a comprehensive understanding of how and why a tree species differs across its range. Along with the discussion of these concepts is a review of experiments designed to test the genetic theories (chapter three) and a description of research results on the genetic variation of select angiosperm and gymnosperm tree species (chapter four).

Chapter five applies the concepts and research of chapter three and four to silvicultural practice. Rather than cover the full realm of silviculture, however, Dr. Morgenstern focuses on the one area of silviculture most influenced by tree genetics, reforestation. And rather than discussing breeding programs, Dr. Morgenstern covers more basic concerns: controlling seed origin; seed zones and seed transfer; and species introduction. In each of these areas, Dr. Morgenstern brings up cautions and examples to make the connection between research and application.

The final chapter is a cautionary note on conserving genetic resources. Dr. Morgenstern realizes the importance of plants in filling the basic needs of society. He also recognizes the value of genetic diversity and the need to preserve native plants in their natural environment. Dr. Morgenstern lists why conservation is important and then suggests ways to implement gene conservation programs.

Dr. Morgenstern has taken a complex field of study with a long history and delivered its essence to his readers. He backs up clear explanations of genetic concepts and theories with a comprehensive Literature Cited section, 30 pages of documents from around the world and across

generations. He focuses on a small area of genetic research and application; how and why forest trees show genotypic and phenotypic variation across their ranges. The reader is left with an overall understanding of geographic variations with forest trees and the ability to delve into literature of more specific interest.

I identify the intended audience of this text as undergraduate and graduate students of forest genetics, and resource managers interested in the hows and whys of variations they see in practice. The book, I believe, holds little for the intermediate or advanced forest geneticist, except possibly as a literature source. With these audiences in mind, I would have liked to have seen a glossary for terms defined in the text. While an index is provided, a glossary would have made reading easier and more comprehensible.

While Dr. Morgenstern has done a laudable job synthesizing genetic concepts, silviculturalists should not read this book expecting a wide range of these concepts applied to management situations. Admittedly, silvicultural systems, such as clear-cutting, shelterwoods, and seed tree cuts, have genetic consequences, but these consequences are not covered in the text. Dr. Morgenstern recognizes the relationship between these systems and forest tree genetics, provides several related references, and then clearly states the relationships are not discussed. In this sense, the audiences I've recommended for this book are even more appropriate.

Dr. Morgenstern has compiled and distilled a considerable amount of literature and experience into a succinct and informative text. I believe students of forest genetics and management practitioners interested in understanding the genetic concepts behind forest tree variations would benefit from reading this book.

— Steve Clements
Extension Forester
Oregon State University
La Grande, Oregon 97850

Ecology and Management of Sitka Spruce, Emphasizing its Natural Range in British Columbia

E.B. Peterson, N.M. Peterson, G.F. Weetman, and P.J. Martin, 1997, UBC Press ($75.00). 336 pages. ISBN 0-7748-0561-7

One prerequisite for management of forests to maintain ecological and economic values is thorough understanding of the biology of key species. Sitka spruce (*Picea sitchensis* (Bong.) Carr.) is one such key species over approximately 2500 km of the west coast of North America. The authors of this volume have two objectives, one as broad in scope as the natural geographic range of the species, the other of narrower scope. The first objective is to update previous general treatments of the ecology and management of Sitka spruce. The second is to identify silvicultural manipulations that might increase production of Sitka spruce on British Columbia's Queen Charlotte Islands, near the center of the species' geographic range. The quest to increase production was spurred by the recent creation of a large national park, significantly reducing the area available for timber harvest.

A brief introductory chapter describes the distribution of the species in its natural range and in exotic plantation forestry, and explains the rationale for assembly of information for this review volume. The bulk of the remainder of the text is divided into two chapters. The first of these is entitled "Biology and Ecology of Naturally Occurring Sitka Spruce." The chapter begins by describing the taxonomy, morphology, and variability of Sitka spruce. In British Columbia, spruce taxonomy is complicated by the presence of four native species with overlapping ranges. Helpful information is presented on morphology of the different species and potential zones of hybridization. The largest portion of the chapter is devoted to the geographic distribution and ecological characteristics of ecosystems in which Sitka spruce occurs. Much of this information (and information in many other sections of the book) is organized using the biogeoclimatic ecosystem classification for British Columbia developed by Klinka and others. Thus readers will benefit from familiarity with the biogeoclimatic ecosystem classification scheme. Shorter sections are devoted to regeneration, growth and productivity, soil, nutrient, and mycorrhizal relationships, and abiotic disturbance. The latter section demonstrates that the literature on Sitka spruce as a plantation species in the United Kingdom can inform management in the species' natural range. A recent set of guidelines for minimizing windthrow in British Columbia suggests as one alternative harvesting stands when the trees reach a critical height above which windthrow is likely. The critical stand heights have been derived from observations of plantations in the United Kingdom. There is a fairly extensive section on insects and diseases, noting in particular the prevalence of the white pine weevil (*Pissodes strobi*), which can repeatedly destroy the leader of spruce trees. South of the Queen Charlotte Islands, Sitka spruce is not used for reforestation in coastal British Columbia due to the high probability of weevil attack. The final section of the chapter describes the habitat values of ecosystems containing Sitka spruce for fish, mammals, and birds.

The second major chapter is entitled "Management of Sitka Spruce." There are short sections on natural regeneration and control of competing species. Considerable space is devoted to establishment of plantations, including stock selection, propagation and nursery practices, site selection, site preparation, planting density, and early brush control and thinning. Again the literature concerning Sitka spruce in the United Kingdom is put to good use. Stand-level activities to improve timber yield and quality also receive a large amount of attention. Specific activities include tree improvement, silvicultural systems (with clearcutting the surest method for regenerating Sitka spruce), fertilization, pre-commercial thinning and other aspects of density control, and pruning. Other topics addressed in the chapter include crop planning, estimating site quality, predicting regeneration, growth and yield models and data, management to minimize losses to insects and disease, protection of old-growth forests, and management for wildlife habitat, recreation, and water quality. The book concludes with a short chapter entitled "Sitka Spruce in British Columbia's Future."

Overall, the book is a comprehensive treatment of the basic biology and management issues of Sitka spruce, placed in geographic, ecological,

and economic context. There is some degree of tension between the book's two objectives, and it is not always clear whether particular statements apply to the entire natural range of Sitka spruce or just to its range in British Columbia. In addition, an attempt to reconcile the biogeoclimatic ecosystem classification scheme used in British Columbia with vegetation classification schemes that apply to Sitka spruce ecosystems in Alaska, Oregon, and Washington might have facilitated comparison of research results. Such comparisons across the range of Sitka spruce may increase in importance with global climate change. Nevertheless, this book is full of detailed and worthwhile information. It is certain to be of great practical value to anyone concerned with management of Sitka spruce within its natural range.

—Steven A. Acker
Department of Forest Science
Oregon State University
Corvallis, Oregon 97331

Plant Dormancy: Physiology, Biochemistry and Molecular Biology
G. A. Lang, Ed., 1996, CAB International, 55 British Pounds (about $90)

The primary means plants use to survive periods of adverse growing conditions is some form of dormancy, *sensu lato*. Dormancy has been an active area of research since at least the time of Julius Sachs, the founder of modern plant physiology. Unraveling the mysteries of dormancy in seeds and buds is important for understanding how plants respond to environmental conditions, and has implications for ecology, forestry, horticulture, and agronomy. While techniques for studying development and release of dormancy have become more sophisticated, many of the questions that have been central to these studies (e.g., what is(are) the mechanism(s) of dormancy release) remain active areas of research.

Plant Dormancy, the result of the *1st International Symposium on Plant Dormancy* held in Corvallis, Oregon, provides a comprehensive view of current research on seed and bud dormancy. The volume is divided into sections on seed and bud dormancy systems (I & II), physiology (III), biochemistry (IV), molecular biology (V), and modelling (VI). It is divided equally into chapters on seeds and buds. The chapters vary considerably in their detail with some being overviews and others being essentially research papers. It would have helped to have some synthesis chapters at the end of each section as well as at the end of the book to draw things together and, more important, to point out areas in need of further research.

Several chapters do a good job of placing the topic in a broader perspective. Leopold's introductory chapter, Natural History of Seed Dormancy , starts off with a statement that I think all biologists should keep in mind: ... the focus on reductionism has the potential to cause science to drift inexorably away from the real biology of living organisms, increasingly separating us from the natural history of our science. I wish more of the chapters had kept this admonition in mind so that the reader could come away from each chapter with a sense of how the details related to the whole. Nonetheless, the reader who perseveres through all the chapters will come away with a better understanding of what is known about plant dormancy and the difficulties in studying its control.

The first two sections are essentially parallel treatments of dormancy systems and concepts in seeds (I) and buds (II). The chapters in these sections present information at the organ level and provide a basis for the later chapters. I found these chapters among the most interesting and useful because several provided a review of current understanding of plant dormancy in the areas covered. I particularly enjoyed Leopold's chapter on the Natural History of Seed Dormancy for its emphasis on seed dormancy and germination as system responses; Dennis' comparison of dormancy mechanisms in seeds and buds; and Crabbé and Barnola's chapter describing A New Conceptual Approach to Bud Dormancy in Woody Plants . The other five chapters in these two sections will prove interesting and useful to other readers.

The next three sections explore finer and finer details of the dormancy process and, therefore, move further down the reductionism ladder. Nonetheless, they provide useful insight into details of critical problems in our understanding of dormancy, including hormone relations and gene expression. With my research interests in tree growth, I found the chapters on conifer buds (Conifer Bud Dormancy and Stress Resistance: a forestry perspective by Bigras and Early Development of Bud Dormancy in Conifer Seedlings by MacDonald) to be particularly useful. The section on biochemistry (IV) was dominated by studies on seeds and embryos, most likely reflecting the relative ease of doing biochemistry on seeds relative to buds. However, the chapter on the biochemistry of dormant buds in tubers provided an interesting look into biochemical control of bud activity through changes in sink strength of nearby tissues.

Section V on molecular biology provides a set of four snap shots of research in gene expression during dormancy. These chapters describe the application of recently developed techniques for investigating gene expression. In some ways this is the most detailed, and reductionist, level of research in biology and, therefore, most removed from the system-level approach mentioned in the first chapter. However, one chapter that I

found personally interesting and useful was the one by Colman and Chen (Photoperiod-associated Gene Expression during Dormancy in Woody Perennials) in which they describe the control of nitrogen/protein storage as related to plant dormancy.

The final section, Dormancy Modelling (VI), presents three models dealing with dormancy in seeds or buds, each emphasizing different aspects. Throughout this section the authors make a point of the fact that determining when a bud or seed is dormant (endogenous dormancy) vs. simply not growing because of environmental conditions (ectogenous dormancy) is not possible with current methods. The first chapter in this section (Population-Based Models Describing Seed Dormancy Behaviour: Implications for Experimental Design and Interpretation by Bradford) puts forth a strong argument for using techniques of population biology to study seed dormancy. Briefly, this method of analysis assumes that the depth of dormancy in a seed population is distributed over a range from greater to lesser dormancy and that this distribution shifts with various dormancy-breaking and inducing treatments. The second chapter in this section used the idea of population variation to investigate control of seed dormancy. The final chapter investigates control of bud dormancy using a model developed to explain the relationship of dormancy to temperature. All three chapters provide worthwhile insights into the control of dormancy.

This volume provides a good review of current topics in plant dormancy. It is organized in a logical manner to take the reader from the general to the specific. The lack of direct connections among the chapters is regrettable, but not unusual in proceedings volumes. Each chapter is basically self-contained, making it useful as a reference for researchers in dormancy and for those who wish to explore current thinking in the area. As an exploration of current thinking in dormancy *Plant Dormancy* will be useful to a wide range of students and researchers interested in control of plant growth and a good addition to botanical research libraries. The editor, G.A. Lang, and the various contributors are to be commended for their efforts.

—James A. Weber
U.S. Environmental Protection Agency,
NHEERL-WED
200 SW 35th St
Corvallis, Oregon 97330

Macrolichens of the Pacific Northwest

Bruce McCune and Linda Geiser, 1997, Oregon State University Press ($25.95)

Oregon State University Press. 386 pages. (ISBN 0-87-71-394-9) paperback: contact OSU Press: 541-737-3166, fax 541-737-3170. $25.95 plus shipping ($2.50 book rate).

Can you see the forests for the trees? Can you see the lichens for the trees? If not, you will after using this new lichen flora. *Macrolichens of the Pacific Northwest* is the first regional lichen key in the United States that is fully illustrated by color photos. These color photos make the book useful to both expert and novice botanists alike. This is one of the few books on lichens that every general ecologist in the Pacific Northwest will want. Over 200 taxa are illustrated with color photographs as well as additional line drawings. The detailed line drawings clarify diagnostic features between species by providing a close-up or side by side comparision of specific features.

Dichotomous keys which include only Pacific Northwest macrolichens make for much easier specimen identification than books covering a larger geographic area. In the past, one had to rely on Mason Hale's (1979) book *How to Know the Lichens*, which covers all of North America. Some of the species in the Pacific Northwest were mentioned only under descriptions of similar wider-ranging species (e.g. *Ramalina subleptocarpha* is discussed under *Ramalina farinacea).* The keys are well written and consistent in their presentation of morphological features.

There are keys to the family and genera of lichens as well as detailed species keys for each individual genus. This makes it possible to start either at the beginning or jump ahead to the generic level. This organization helps one learn and over time the reader will better understand the generic concepts and morphology. The text is arranged alphabetically by genus followed by species, so one rarely needs to turn to the index. The photographs and line drawings are on the same page as the species descriptions, which reinforces the familiarization process.

What are macrolichens? They are the typically larger foliose and fruiticose lichen growth forms that can be distinguished without the use of a high magnification light microscope. They are often the conspicuous species seen growing attached to trees or growing over the ground in the forests of the Pacific Northwest. Microlichen species, as the name implies, are the smaller crustose lichens on rocks or closely adnate to bark which require close examination by light microscope.

This book provides much basic information on lichen biology. What are lichens? Why are they important? How lichens function, reproduce, grow, and disperse are all discussed to some extent and more in-depth references on these topics are included. An illustrated glossary is provided as well as these appendices: 1) Acronyms and nomenclature; 2) Collecting and identifying lichens; and 3) Lichens and air quality.

Each individual species has the name in bold at the top of the page followed by its description, an air pollution sensitivity rating, the geographic range, substrate, habitat, and "notes". " Notes" includes comments on similar species and their distinguishing characteristics, as well as ecological and geographical differences. This section also includes identification tips and information on the ecological, indicator, and ecomonic role of the species. This book is the best source for regionally based air pollution sensitivity ratings for these lichen species.

If you would like to know which lichens are good indicators of old-growth forests or which contribute high nitrogen input to the forest, you should obtain *Macrolichens of the Pacific Northwest.* You will soon learn that lichens are in every habitat you visit and knowing more about them will increase your appreciation for the world around you. What can be easier and more enjoyable than the availability of color photographs to augment traditional dichotomous keys? McCune and Geiser have organized an excellent treatment on lichens, but photographers Sylvia and Stephen Sharnoff, who's names are listed inside the cover, contributed greatly to the usefulness of this book through their outstanding photography. Lichens are small and difficult to photograph, but the Sharnoffs have set a standard that will be hard for others to even approach.

—Roger Rosentreter, Ph.D.
Bureau of Land Management
1387 S. Vinnell Way
Boise, Idaho 83709

Red-winged blackbirds: Decision-making and Reproductive Success.
Les D. Beletsky and Gordon H. Orians. Chicago University Press, Chicago, Illinois 1997, ISBN: 0226-04187-5 (paper, $21.95); 0-226-04186-7 (cloth, $65.00).

In their monograph, Les Beletsky and Gordon Orians discuss the reproductive success of that most familiar of songbirds, the red-wing. Orians first began to study blackbirds in the late nineteen fifties, and this work has illuminated almost every major aspect of behavioral and population ecology. Orians' early studies focused on social systems, and culminated in the 1980 monograph, *Some Adaptations in Marsh Nesting Blackbirds*. At about this time, Orians was joined by his younger colleague Les Beletsky in work on individual life histories of the red-wing and their social context. This book reports the fruits of the authors' 16-year collaboration.

At the time this work began, there was much interest in the factors determining the reproductive success of individuals, particularly over a lifetime. A key issue then and now is whether wild animals "choose" carefully which partner(s) to breed with, where to breed, how much to invest in each breeding event, and whether to adjust these choices from year to year to optimize lifetime breeding success. Alternatively, individuals make few real choices in their breeding lives, and chance plays the determining role in how many offspring they rear. The red-wing is a suitable subject for such studies because it is conspicuous, easily caught, and it has sex-specific life histories. Females breed as yearlings, but males generally do not, although they are physiologically capable of breeding. Red-wings are also sufficiently short-lived that individuals' life-spans can be covered within the limits of the patience of a committed investigator.

The study took place in eight neighboring marshes in the Potholes of eastern Washington State. This is a seasonally and annually variable environment with cold springs and hot summers, and it changed markedly during the study, because of destruction of marsh vegetation on some lakes by beavers. The principal key to the success of the study was an extensive banding program, where thousands of redwings were trapped and individually marked at feeding sites near the marshes, but the authors and their colleagues used a full range of modern methods, including DNA fingerprinting, manipulations of sex hormones, and radio telemetry.

In the first main part of the book, the authors first consider the reproductive decisions of females. These include: when to start breeding, when to stop, whether to breed in a pocket or strip marsh, and whether to return to an old territory or to seek a new one. Female red-wings turn out to be conservative in most of their choices. They start to breed as yearlings, delay laying for about a month after arriving, and generally return to a previously used marsh and territory, even if other more productive territories are available nearby. They pay little attention to the identity of their male partner, although they do choose sites where clusters of familiar males live; these neighbor males sire about a third of the average female's offspring, according to DNA studies by Elizabeth Gray. Females appear to stop breeding before poor environmental conditions enforce it. Their breeding success is limited by several environmental factors: bad weather, habitat damage by beavers, competition with yellow-headed blackbirds for nest sites, and the effects of predators and brood parasitic brown-headed cowbirds on nesting success.

Males, like females, settle close to their birth places, but one or more years later. As in females, reproductive success is mainly determined by an individual's longevity. Because of the high degree of polygyny in red-wing populations in eastern Washington, about half of all males are non-territorial "floaters", that do not reproduce until they gain breeding territories, which may not be until they are five or six years old. Obtaining and keeping a territory is thus the key to male breeding success. Beletsky and Orians discuss in detail how floaters contest for territories. Most do so by gaining vacant territories at the outset of each season, but some fight their way in between existing owners. One might expect owners to be better fighters and in better physiological condition than floaters, but experiments where males were trapped and removed temporarily for one to nine days, revealed that most floaters can defend a territory successfully against the original

owner, provided they have a few days of ownership experience. The psychological advantage of ownership thus generally outweighs any individual differences in fighting ability. In declining populations towards the end of the study, there were few floaters, and replacements for removed territory owners were generally previously territorial birds who moved to new sites.

Synthesizing the reproductive decisions of male and female redwings, Beletsky and Orians argue that both sexes are capable of wise tactical decisions that improve their breeding success, but that the predictive information provided by a highly variable environment is often too poor to allow better decisions to be made. As a result, redwings often stick with their past breeding sites and mates, even when they could seemingly do better by moving to other sites. Floater males should benefit by learning about the strength of territory owners and selectively challenging the weaker ones, but they do not often do this. While these patterns appear to result in high reproductive success having as much to do with chance as with smart decision making, the authors argue that redwings are not "bird brains", but that their environment is simply too unpredictable to allow them to use their considerable intelligence. I suggest an alternative perspective that, because breeding success increases almost linearly with life span, the key to lifetime breeding success lies more in the many small decisions that influence survival rather than in a few key decisions concerning reproduction.

Overall, I liked this well-written monograph, with its clear data presentation and sensible interpretation of data. While most of the material is fairly narrowly focused around the red-wing, useful comparisons are drawn with red-wing studies elsewhere, and the final chapter draws some interesting general conclusions. I would, however, have liked to learn more about predation on nest contents and brood parasitism, as these seemed to be stronger influences of female reproductive success than settling order, a subject treated in much detail here. A topic that the authors did not study, and which I suspect would be of interest, is the survival of fledglings. I suspect that it is highly variable in early breeders, and poor in very late breeders, thus explaining the delay in the start of breeding, and the sudden end to breeding when conditions still appear to be optimal. I would also have liked to see more personal touches in the narrative, and to hear more about the nature of the authors' collaboration. I guess that this is primarily Beletsky's book, with Orians playing only a minor role, but I could be wrong. In conclusion, this is a fine piece of work, and good value in its paperback edition. I recommend it with enthusiasm.

— James N. M. Smith
Dept. of Zoology
University of British Columbia
6270 University Blvd.
Vancouver, B.C. V6T 1Z4
Canada

Biodiversity II: Understanding and Protecting Our Biological Resources
Marjorie L. Reaka-Kudla, Don E. Wilson, and Edward O. Wilson, eds., 1997, Joseph Henry Press ($34.95)

Since the first BioDiversity collection in 1986, and in part because of the its publication, there has been a flurry of activity in both research and policy arenas on biodiversity. Numerous articles have been written on various aspects of biodiversity. The Convention on Biodiversity is a prominent international policy iniative. Rather than needing to call attention to biodiversity as did the first volume, the current volume suggests ways to organize and use the vast amount of information currently being generated as well as propose strategies to efficiently collect the even greater mountains of information about biodiversity that are potentially important. Biodiversity, according to some, is everything; "from the genes within a single local population or species, to the species composing all or part of a local community, and finally to the communities themselves that compose the living parts of the multifarious ecosystems of the world." (E.O. Wilson, page 1). A large task awaits. How can biologists collect, organize and utilize information about "everything" in a cost effective manner?

This book is a collection of 33 papers that was organized by the Consortium for Systematics and Biodiversity, which includes various research organizations in the Washington, DC area. A majority of chapters were written by contributors who work at Consortium member institutions. The book is organized into seven parts, including an introduction and conclusion. The five substantive sections of the book focus on: a) the extent of biodiversity, b) causes and rates of extinction, c) understanding and using biodiversity, d) strategies to collect and apply information, e) the information infrastructure.

The sections on the extent of biodiversity and the causes and rates of extinction are familiar topics in the biodiversity literature. The chapter by Nigel Stork contains a useful and sober summary of the state of knowledge about the current extent of biodiversity and to a lesser extent its rate of decline. The chapter by Marjorie Reaka-Kudla about coral reef biodiversity, contains estimates of the extent of biodiversity in reef systems, and perhaps as importantly, illustrates the thin basis of our understanding upon which such estimates are based at present. Chapters by David Stedman and Scott Wing provide evidence on avian extinctions and extinctions in response to past climate change. The change in tone from these chapters to the chapter by Norman Myers is striking. Myers points to large impending losses of biodiversity and the urgent need to act to protect what remains. This chapter is less a careful examination of data and more a call to arms.

The middle sections, on understanding biodiversity and strategies to collect and apply information, which make up almost half of the chapters in the book, are more difficult to characterize. The contributions in these sections are quite diverse, ranging from systematics to evolutionary theory to biotechnology to sustainable development. In part because of this diversity, a consistent theme does not emerge from this portion of the book. These two sections may be a metaphor for the entire book and the larger effort to make sense of biodiversity. Without careful thought about how to put the pieces together, one is left with a collection of interesting facts but without a clear storyline. Given the vast amount of biodiversity information, it is important to have larger objectives guide the research and a structure in which to make sense of results. Even without a plot, however, there are many interesting and useful papers in these sections. Readers will probably pick and choose chapters to read that are of particular interest to them. I found the two chapters by Carol Bult et al. and Timothy Friedlander et al. that describe methods for cataloguing genes and how these methods can be used to build databases and phylogenies to be of great interest. In other chapters of interest, Michael Scott and Blair Csuti describe the GAP program agenda to collect information and set conservation priorities, and Douglas Miller and Amy Rossman discuss the application of biodiversity and systematics to agriculture.

In a provocative chapter that provides a bridge between the middle sections and the final section of the book, Daniel Janzen lobbies for All Taxa Biodiversity Inventory (ATBI) as superior to other potential approaches for collecting and using

biodiversity information. An ATBI seeks to provide a complete inventory of all taxa for a limited geographic range. In the very next chapter, Quentin Wheeler and Joel Craycraft argue for the approach in *Systematics 2000*, which focuses more on the study of taxa where appropriate and does not target specific areas. This debate brings out a central issue of the book: how best to proceed with the large task of organizing the study of biodiversity? The juxtaposition of the two chapters allows the reader to make their own comparison of which approach is likely to be more beneficial.

An issue that is addressed, mostly tangentially, are the reasons to conserve biodiversity. For most of the contributors, the goal of conserving biodiversity is a given. Whether this is because there are important human benefits to be derived or because biodiversity is intrinsically valuable is often not made clear. Janzen advocates a "use it or lose it" strategy, meaning that the way to save biodiversity is to find ways to utilize and make biodiversity valuable. Others have argued against basing conservation on economic or utilitarian grounds (e.g., Ehrenfeld in the first BioDiversity collection). In going beyond the biological community, however, it is important to clearly state the importance of conserving biodiversity, especially if the repeated pleas for additional funding for conservation and research are to heeded. In this effort, other disciplines not represented in this collection, such as economics and philosophy, will have much to contribute.

—Stephen Polasky
Department of Agricultural and Resource Economics
Oregon State University
Corvallis, Oregon 97331-3601

Upstream: Salmon and Society in the Pacific Northwest

Committee on Protection and Management of Pacific Northwest Anadromous Salmonids, 1996, National Academy Press ($44.95)

Is there really much more that could be written about the decline of salmon in the Pacific Northwest? After all, the scientific aspects of the salmon decline have been reasonably well known for many years. Sure, we learn a little more each year about the biology of salmon, but the salmon "problem" doesn't have a lot to do with fish or even science. It is about tradeoffs—difficult, unpopular, wrenching tradeoffs. If only it were otherwise. Concern over the decline of salmon is an example of a wickedly challenging ecological policy question for which there are no easy answers, nor solutions that only require spending more money.

How, then, is it that we need another scientific review of the decline of Pacific salmon? The Committee on Protection and Management of Pacific Northwest Anadromous Salmon was formed in 1992 by the National Research Council at the request of Congress. The committee's charge was to evaluate the options for long-term sustainability of salmon stocks and the economic and social consequences of such changes, ground that had been plowed by many others.

The technical facts of the case are well known. Pacific salmon (including steelhead and sea-run cutthroat trout) have disappeared from nearly half the area of the U.S. Pacific Northwest (Washington, Oregon, Idaho, and Northern California) where they occurred as recently as a century ago. Many of the remaining runs are severely depressed. Even most of the significant runs that still exist are composed predominantly of hatchery-bred fish. The causes, both oceanic and land-based, for the decline are reasonably well known although there continues to be vigorous scientific debate as to the relative ranking of the causes.

The specific directives issued to the committee were to (1) assess the state of salmon stocks in the Pacific Northwest, (2) analyze the causes of their decline, and (3) analyze the options for reversing the apparent downward trend. The committee was not asked to recommend what, if anything, society *should* do, but to inform the public and Congress of what the likely consequences would be for various options under consideration. Items 1 and 2 are the subject of other technically sound reviews. Item 3 could be interpreted as either part of a larger public policy question of which salmon are only one of many tradeoffs, or as a purely "salmon" issue with the societal decision options being unrealistically constrained.

The committee's directives essentially defined the salmon "problem" as it is typically treated—a "fish" problem rather than a public policy problem. The tacit dictum is "If we just had more scientific information, we could solve the problem, perhaps even not too painfully." What usually follows the results of one analysis of the salmon problem is a call for another study with better, more insightful scientists who will be able to solve the problem. To a large degree, the membership of the committee reflects this orientation. The members are all eminent professionals who represent some of the best in the fields of fisheries, limnology, aquatic biology, zoology, hydrology, genetics, molecular biology, biometrics, and conservation biology. To be sure, there are a few members with professional interests in natural resource economics, anthropology, and public policy, but the committee membership is pretty much a "biologist's committee."

But the salmon "problem" is not really about the decline or loss of salmon runs, the appropriate role of hatcheries, nor even whether certain salmon stocks should be listed as threatened or endangered. Rather it is a clash of an array of values and preferences, many of which are mutually exclusive. Society and individuals make choices within ethical, economic, and political contexts. Salmon are simply one of many competing values and preferences in the marketplace of democracy and public policy.

The book is organized into 15 chapters that collectively provide an admirable summary of what is known about Pacific salmon, especially life history, genetics, geography, ecology, role of human influences, and the status of the salmon stocks in different geographic areas of the Pacific Northwest. Other chapters deal with the influences of habitat alteration, dams, fishing, and hatcheries. This material is not new but is presented in a concise, readable way.

There are also chapters and sections that deal with public choice issues and how those choices affect salmon, but this material comprises a small portion of the book. The chapter on values and institutions is especially helpful, but does not go beyond a general discussion of the issues. From my perspective this is a weakness. The book in the aggregate reflects, perhaps appropriately, the committee's charge: to provide a fairly narrow definition of the salmon problem. However, the real societal tradeoffs are agriculture vs. salmon, energy vs. salmon, affordable housing vs. salmon, personal mobility vs. salmon, population growth vs. salmon, tax policy vs. salmon, individual rights vs. collective rights, and inter- vs intra-generational tradeoffs. There is, of course, no correct scientific or "right" decision to any of these tradeoffs, although scientists can provide an assessment of the consequences of the various alternative decisions. A little reality might help; if the Pacific Northwest continues to grow as it has for the past 50 years, the area will be inhabited by 65 million people.

In spite of its limitations, this is a very good book and worth the purchase price to anyone interested in salmon biology and policy. It is unfortunate, however, that such a highly visible effort did not concentrate on the heart of the salmon policy question, societal tradeoffs of which salmon is only one of many. Perhaps its time to look at alternatives to restoration of salmon, such as managing for fish species better adapted to the highly modified aquatic and terrestrial environments of the Pacific Northwest.

—Robert T. Lackey
U.S. Environmental Protection Agency
200 SW 35th Street
Corvallis, Oregon 97333

Fish Stress and Health in Aquaculture
G. K. Iwama, A. D. Pickering, J. P. Sumpter, C. B. Schreck (eds.), 1997, Cambridge University Press. (Cloth, $90.00)

The role of stress in altering physiological homeostasis in cultured fish has received increasing attention from researchers in recent years, as the economic importance of aquaculture has grown. *Fish Stress and Health in Aquaculture* (278 pages) provides a useful, in-depth survey of the resulting body of scientific literature. The ten chapters were written by researchers who have themselves contributed many of the seminal published articles in this field.

The book begins with a discussion of the history of the stress concept and its application to fish. The author (Barton) points out that stress responses are not necessarily detrimental, but are adaptive responses to situations threatening immediate injury or death. Stress responses can become maladaptive, however, when stressors become chronic or repetitious, as under intensive fish culture conditions. This chapter also synopsizes the status of current research on stress in finfish. The following chapter (Wedemeyer) considers the effects of rearing conditions on the health and physiological quality of fish cultured under intensive conditions: stressors are considered under the headings of water quality, culture procedures, and biological interactions (aggression and dominance). The role of stress in lowering resistance to infectious disease is reviewed. A later chapter (Balm) treats the effects of stress and stress hormones on immune defenses and presents evidence favoring the integrated interaction of the fish endocrine and immune systems, a model now widely accepted for the mammalian immune system.

A chapter on the endocrinology of stress (Sumpter) begins with a description of the classical hypothalamo-pituitary-interrenal (HPI) axis, but broadens this simple picture with examples of the complex interactions and control mechanisms now known or hypothesized to occur at all levels of the HPI axis. Another chapter (Pankhurst and Van Der Kraak) reviews the effects of stress and cortisol on gonadal steroids, vitellogenesis, and gamete quality. This chapter also reviews the effects of stress on growth, but, although somatic growth is consistently reduced by stress or cortisol treatment, the processes responsible are not yet clear because growth is regulated by a multitude of interacting factors.

A chapter on alterations of ionic and osmotic balance in stressed fish (McDonald and Milligan) deals primarily with regulation of blood and whole-body sodium and choride ion levels. The authors distinguish between a "simple" stress response (mediated largely by increased blood adrenaline levels, resulting in a net branchial efflux of ions) and "compound" responses, which, in addition to the adrenergic response, involve vigorous activity, toxic injury, or physical injury. Compound stressors elicit more complex and protracted ionic and osmotic disturbances, and may also affect acid-base balance.

As with physiological responses to stress, behavioral responses to stress can be adaptive or, if stressors are inescapable or repeated, become maladaptive. Chapter 6 (Schreck, Olla, and Davis) reviews stress-induced alterations of behavior, including effects on perception and avoidance of unfavorable environmental conditions and predators, swimming and feeding activity, habitat use, and aggressive interactions. The authors point out the potential value to aquaculturists of additional research on the stress responses of larval fish.

Although measures for reducing the deleterious effects of stress are suggested throughout the book, adverse stress responses are unavoidable in intensively cultured fish. Consequently, attempts have been made to develop strains of fish with attenuated stress responses (Chapter 7, Pottinger and Pickering). This intriguing work in in its early stages, but results to date indicate that selective breeding for reduced stress responsiveness is feasible. Furthermore, reduced stress responsiveness has been shown to correlate with greater resistance to some fish pathogens. Another approach to alleviating the adverse effects of stress is through improvements in the diet of cultured fish (Fletcher); fish diets are presently formulated to prevent nutritional deficiencies and to provide for optimum growth, but relatively few studies have been done to establish optimal nutrient concentrations for mitigation of the deleterious effects of stress. The studies reviewed by this chapter deal with the effects of dietary concentrations of carbohydrates, proteins, and lipids and of various minerals and

vitamins on immunocompetence and disease resistance.

The final chapter (Morgan and Iwama) addresses the special problems and limitations associated with assessment of stressed states under field conditions. A number of simple and reliable field methods for measurement of physiological indices are described. This chapter would be improved by discussion of biases introduced by extended anesthesia of fish prior to sampling (field conditions often require that fish be anesthetized in batches, rather than individually) and by extended storage (minutes to hours) of blood samples.

Throughout the book, relevant material presented in other chapters is cross-referenced, providing a degree of continuity and integration that is often lacking in multi-authored volumes. Over 900 citations are provided, the majority to papers published since 1990. This book will be a valuable aid to researchers wishing to improve their understanding of the stress physiology of fish.

—James L. Congleton
Idaho Cooperative Fish and Wildlife
Research Unit
Biological Resources Division, USGS
Department of Fish and Wildlife Resources
University of Idaho
Moscow, Idaho 83844-1141

The Evolution of Social Behavior in Insects and Arachnids

Jae C. Choe and Bernard J. Crespi, Eds., Cambridge University Press ($100.00)

The Evolution of Social Behavior in Insects and Arachnids is an important resource for anyone interested in studying the evolution of social behavior in invertebrate or vertebrate taxa. Anyone that has delved into the topic of social behavior in insects is aware of the impressive and sometimes overwhelming amount of literature that has focused on eusocial insects with a specific emphasis on the Hymenoptera. Choe and Crespi have taken a unique approach to this broad topic by presenting the full spectrum of social behaviors in several insect groups and the arachnids. Looking beyond traditional taxa and conventional inner-relatedness paradigms this book presents potential ecological, demographic, and phylogenetic relationships that may contribute to the evolution of social behavior.

The main purpose of this book as stated by the editors, is to explore the factors that cause variability and diversity of social behavior in animal systems. As the spectrum of social behavior is greatest among arthropod taxa, they serve as excellent model systems in which to investigate the evolution of social behavior. The great diversity of social behavior in and among insect groups also presents several problems which this book addresses. A singular hypothesis that sufficiently explains the maintenance and evolution of social behavior for all groups is unlikely. The Hymenoptera serve as a prime example, bees and ants exhibit haplodiploidy and are more related to each other than to their queen. While this condition may sufficiently explain how Hymenopteran insects can maintain social colonies it does not provide a mechanism that explains the evolution of eusociality. Furthermore, several eusocial groups do not exhibit haplodiploidy. Termites are eusocial and are diploid as are a myriad of other insect groups that exhibit diverse forms of social behavior. Thus, the objective of this book is to investigate the numerous ecological, demographic, and genetic factors that contribute to the evolution of social behavior in separate insect groups, and to broaden the definition of sociality in arthropod taxa to allow for comparisons with the social behavior of vertebrates.

The introduction and first chapter "Are behavioral classifications blinders to studying natural variation." are exemplary in that they concisely and clearly introduce the field, related terms and vocabulary. I wish that this book had been available when I first began to research and investigate topics in this field. The clear descriptions and explanations of various terms such as the inclusive fitness inequality (rb-c>0), reproductive skew, and how they are related to current theories and questions in the field is excellent. In addition, the introduction and first chapter give the reader the historical background and perceptual framework to fully appreciate the rest of the book.

The remainder of the volume consists of 22 chapters which introduce and discuss different questions relating to the evolution of insect social behavior. The topics are very diverse and broad in scope. Chapters include: a monogram of primitive social behavior, factors influencing colonial nesting, cooperative brood care, detailed phylogenetic analyses of social behavior within a single taxon, and the evolution of maternal and paternal investment. One chapter is even dedicated to comparing cooperative breeding strategies in vertebrates and wasps.

In my opinion the chapters could be better organized. The chapters are loosely grouped by taxon instead of by subject. As an example, the arachnids are treated sequentially at the end of the book and the Hymenoptera are treated in consecutive chapters. Each topic tends to be unrelated to the following chapter and this makes the reading somewhat choppy and impedes the flow of the book. This small problem in organization does not make the topics of discussion any less interesting or intriguing. The editors appear to have been aware of this problem and have added a final summary chapter which attempts to bind together all of the topics discussed into a cohesive framework.

To the editors' credit they clearly present the numerous and broad array of taxa which exhibit varying degrees of social behavior. Eight of the 24 chapters deal with the more common groups in this field (bees, ants, wasps, termites and aphids). All of these chapters are interesting in their own right and serve as excellent introductions to each group. Anyone interested in the diversity of social behavior in these taxa and the current

questions being asked with these groups will find *The Evolution of Social Behavior in Insects and Arachnids* exceptional in this regard. I particularly enjoyed the chapter on social conflict and cooperation among founding ants by Choe and Perlman. The remaining chapters deal with several interesting and more exotic taxa that exhibit social behavior. A few of the topics discussed include paternal and maternal care in hemipterans and cockroaches, social behavior in gall thrips, sub-social and social behavior of several beetles, and even mites. I found the last two chapters on the evolution of sociality in spiders to be two of my favorite chapters. The authors present a clear case that colonial web-building in spiders is a result of constraining ecological factors related to prey abundance and habitat. While I was aware of cooperative breeding and prey-capture in spiders I was unfamiliar with the literature and the second to last chapter by Aviles is an excellent review.

One chapter in this book that deserves specific mention is Brockmann's essay comparing cooperative breeding strategies in wasps and vertebrates. I found this chapter to be exceptionally well written and informative. Brockmann's comparisons of the breeding strategies of Florida scrub jays, and other cooperative breeding birds in relation to the cooperative breeding strategies of several species of social wasps is new, unique and refreshing. This chapter focuses on the role of the ecological constraint model in cooperative breeding and will appeal to anyone interested in the field of behavioral ecology and social behavior of animals. This chapter is a perfect example of what Choe and Crespi have attempted to do in this book. By broadening the scope of the question to include the evolution of social behavior in all animal systems Brockmann gains insights that previously would have remained elusive.

Overall I think that Choe and Crespi have succeeded in providing an exceptional addition to the literature on social behavior in insects and arachnids. To my knowledge this book is the first of it's kind to focus completely on the evolution of social systems in invertebrates. Future researchers and graduate students interested now have a comprehensive volume that reviews the current literature and provides insightful new questions that probe the evolution of social behavior in insects and arachnids.

—John Melville
Zoology Dept.
Oregon State University
Cordley Hall, Rm. 3029
Corvallis, Oregon 97330

The Evolution of Mating Systems in Insects and Arachnids

Jae C. Choe and Bernard J. Crespi, Eds., Cambridge University Press ($100.00)

The Evolution of Mating Systems in Insects and Arachnids takes a very fresh and intelligent approach to mating systems questions across an impressive array of insect and arachnid taxa . The book presents a comprehensive assembly of the latest and most intriguing research in mating systems evolution. It provides a background for each system discussed and delves into provocative evolutionary questions and potential mechanisms that have affected them. Especially refreshing was the attention to both female and male evolutionary perspectives throughout the book. This balanced and subjective approach is a welcome deviation from a tradition that has often overlooked or discounted female choice in sexual selection.

The main purpose of the book, as stated by the editors in the introduction, is to synthesize theory and observation in order to explore compelling evolutionary questions across and among many different groups of insects and arachnids. It is intended to update and complement past and recent work on mating systems and sexual selection, and also to address evolution in a wide range of systems using a taxon-centered approach. They accomplish this with a large collection of essays by the leading experts in a very broad range of insect and arachnid mating systems.

The first chapter on evolutionary perspectives familiarizes the reader with vocabulary and definitions as well as substantial background for understanding and appreciating the rest of the material. This initial presentation of the conflicts that exist between males and females for control over mating is extremely thought provoking. The discussion that develops regarding the evolutionary implications of intersexual and intrasexual struggles raises many fascinating questions that lead nicely into the main text of the book.

The essays that follow, arranged into 19 chapters, each deal with a different taxonomic group and the particular questions and problems that make that group an interesting and appropriate model for study. The text then begins by providing an introductory framework upon which the remainder of the book builds. The format for each chapter is primarily the same: 1) a review of the systems that exist within a particular taxonomic group, 2) a discussion of factors that have influenced and shaped these systems (and continue to do so), and 3) ask new questions for future study and identify the most interesting new areas of research.

Each chapter provides a very thoughtful and comprehensive review of each topic to establish for the reader a perspective on the mating systems within and across the group and the evolutionary pressures they may face. References to older literature are usually dealt with in an innovative manner, with many more new questions arising from old information.

The variety of taxa covered gives the book a great deal of breadth. Wildly interesting and less familiar groups ("antlered" flies, salticid spiders, pseudoscorpions, Zorapterans) along with those well-known (butterflies, moths, katydids, crickets, grasshoppers, fireflies, water striders, etc.) are all demonstrated to be excellent models for future research. As with any book with multiple authors, some chapters are more interesting or have a better flow than others, but each accomplishes the objectives of the editors as stated in the introduction. Chapters that I found particularly enthralling were those on female choice in leaf beetles (Dickinson, Ch. 9) sexual selection in pseudoscorpions (Zeh and Zeh, Ch. 19) and mating systems in cannibalistic jumping spiders (Jackson and Pollard, Ch. 20), this last being my favorite chapter of the entire book.

The variety of evolutionary topics addressed is very impressive. Research is presented in many forms on each component of the mating sequence as described in the first chapter. For instance, rapprochement and pair formation is discussed in the chapters on reproductive strategies of crickets, firefly ecology, mate signalling in moths, lek formation, and to some extent the chapters covering resource defense polygyny in grasshoppers, parasitoid mating systems, and swarming insects. Courtship is a major topic in many chapters but given particular attention in the chapters on cryptic female choice, the evolution of courtship feeding in crickets and katydids, Zorapteran mating systems (which involve edible nuptial gifts), water strider mating systems, Neuropterid mating systems, mate signalling in moths, pseudoscorpion

mating systems, and salticid spider mating strategies. Chapters dealing largely with copulation-related types of research questions include those on odonate mating patterns, mating in leaf beetles, cricket reproductive strategies, courtship feeding in Orthoptera and in Zoraptera, fig-associated wasps, and female cryptic choice. Furthermore, topics such as sexual selection are also discussed in the contexts of the butterfly, pseudoscorpion, leaf beetle, antler fly and territorial grasshopper systems, among others. Population dynamics questions are applied to the skewed sex ratios in mating systems of parasitoids and fig wasps. Many chapters return to the same topics of mate choice by both sexes, intrasexual competition, multiple matings, sperm competition, and the concept of the evolutionary "arms race" between the sexes. There is a great deal of cross-referencing between chapters and this gives the book a very cohesive feel.

The final chapter on sexual conflict and mating systems draws together all of the chapters in a final discussion. It is much like the first chapter in that it asks profound questions and reiterates the importance of research into the evolution of mating systems using the great diversity of insect and arachnid systems. It provides a conclusion for the book while leaving the reader intrigued and eager to learn more.

This book serves as an excellent primer for any student or researcher entering the field of mating system evolution, whether they focus on vertebrates or invertebrates. Many authors draw parallels to vertebrate (and even human) mating systems that make this book all the more appealing to a wider audience. The evolutionary principles and the conflicts between the sexes over control of mating and fertilization are fundamentally the same. I finished reading this book with a revived sense of inspiration regarding my own research (scorpion mating systems). Insects and arachnids provide excellent models for the same questions we have asked about ourselves and other organisms and much can be learned from them. There are complexities and subtleties that are just beginning to be appreciated. This text does an elegant job of furthering the reader's interest in research into these systems.

—Sara Tallarovic
Zoology Department
Oregon State University
Cordley 3029
Corvallis, Oregon 97330

Washington Forest Landscape Management Project—A Pragmatic, Ecological Approach to Small-Landscape Management

Andrew B. Carey, Catherine Elliott, Bruce R. Lippke, John Sessions, Charles J. Chambers, Chadwick D. Oliver, Jerry F. Franklin, and Martin G. Raphael, Washington Department of Natural Resources, Washington Forest Landscape Management Project, Report No. 2 ($10.00)

With increasing and often competing demands being placed on our region's forests, policymakers continue to seek creative and efficient ways to maximize an array of economic and ecological benefits and reduce current conflicts. One such effort, the Washington Forest Landscape Management Project, was charged by the U.S. Congress to explore the advantages of simultaneously managing forests for multiple species of threatened, endangered, and sensitive wildlife over large landscapes and across land ownerships. More specifically, the Project explored ways to meet the needs of wildlife associated with late-seral forests while minimizing impacts on commodity production from Washington's forests. This publication, *A Pragmatic, Ecological Approach to Small-Landscape Management*, is the report of a working group that developed forest management strategies to enhance biodiversity at the scale of the small landscape.

Beginning with the premise that conservation of biodiversity is a foundation for sustainable forestry, the authors present an approach that is implemented through landscape management and that produces regional, long-term benefits. The overall goal of the study was to provide information on some ecological and societal benefits that might be achieved, and costs that might be incurred, by public policy initiatives designed to stimulate management for conservation of biodiversity across all land ownerships. A companion report, *Economic Analysis of Forest Landscape Management Alternatives* (also reviewed in this issue of *Northwest Science*), evaluates financial incentives for motivating landowners to include nontimber objectives along with timber objectives in managing private lands.

The body of the Report is organized into six major sections. The first section introduces the study's objectives, scope, terminology, and concepts. The second section outlines the approach for ecological management of biotic communities. The authors apply their analytical approach in a hypothetical test case, using the Clallam River landscape in the western Olympic Peninsula, which is introduced in section III. Sections IV, V, and VI present the methods, results, and discussion of the test case. The study used a simulation model to project changes in the landscape over 300 years, using real data to start the simulation. Three general approaches to forest ecosystem management were evaluated: the protection-no manipulation pathway, the timber and fiber production pathway (maximization of net present value), and the biodiversity pathway (joint production of ecological and economic goods and services). The most significant result was that maximizing biodiversity through forest management achieved older forest habitat more quickly than other management strategies, and produced significant economic benefit. The study also found that protecting an area by excluding management after a timber harvest appeared to delay the forest's development into older forest significantly longer than if thinning or other management techniques had been allowed. Wildlife diversity was found to differ among stages of forest development and management scenarios, with the lowest diversity found in stages immediately following closure of new forest canopy. Managing to maximize net present value resulted in the highest economic value and the most risk to species. The authors conclude that there is great potential for conserving biodiversity in managed landscapes without maintaining large upland or wide riparian reserves. Important caveats, assumptions, and weaknesses of the analysis are covered in the Discussion.

This study makes several important contributions to the ongoing debate over forest management in the Pacific Northwest, and to applied ecology in general. First, the authors translate ecological concepts that are accepted but often ill-defined into principles, terminology, and approaches that can be used by managers and policymakers. Such practical methods and quantitative measures of ecological values are especially needed for integrated analysis of trade-offs with commodity values. The authors—who include some of the region's most noted experts in

forestry and ecology—develop a conceptual model of landscape management, an expanded conceptual model of forest ecosystem development specific to westside western hemlock/Douglas-fir forest, "biodiversity pathways" for forest ecosystem management, four new indices of forest ecosystem health, and several economic measures.

Secondly, the study focuses needed attention on opportunities to increase ecological and economic benefits from the managed, second-growth forests that dominate much of the Pacific Northwest. As the authors point out, no one yet knows how to conserve biodiversity on intensively managed lands—yet the question is not whether to manage landscapes or not, but whether to manage consciously and purposefully or not. The study's emphasis on managed lands complements strategies for biological conservation that emphasize regional networks of reserves managed primarily for natural values. Indeed, the authors' eight stages of forest ecosystem development recognize old-growth as a unique, natural legacy not achievable through management.

Interdisciplinary approaches are essential to addressing today's critical issues in forest management and policy. In this study, Carey et al. overcame several scientific and practical challenges in integrating biophysical and socioeconomic considerations. Their approach also employs a needed long-term perspective (several centuries). Carey et al. reinforce the reality that optimal solutions will require that decisionmakers adopt this long-term view despite a policy arena that operates on a much shorter cycle. Although the approach also is designed to produce regional, long-term benefits through implementation at the scale of the small landscape, it is unclear how policymakers will "scale up" information from several unique landscapes to assess regional impacts.

Overall, *A Pragmatic, Ecological Approach to Small-Landscape Management* will provide useful guidance to policymakers for formulating incentives to conserve biodiversity on large-landscape and physiographic province bases. Forest managers will find general principles that can be adapted to fit their particular landscapes, rather than a set of analytical tools that can be used straight "out of the box." Carey et al. do a commendable job of synthesizing a large amount of complex information into a conceptual framework and procedures for evaluating the ecological and economic consequences of management and policy alternatives. The approach is applicable to second-growth forests now managed primarily for wood products, as well as to upland and riparian forests managed as late-successional reserves. Scientists will find the report an interesting case study for the application of ecological theory and concepts to a real-world problem. The report will be useful to both general and professional readerships, and in graduate-level courses in ecosystem management. By demonstrating several ways that ecological and economic benefits are not mutually exclusive, the study represents an important step forward from the current polarized debate over forest management. With companion reports, the study points to several incentive-based rather than legislative or regulatory solutions to current forest policy issues.

—Janet L. Ohmann
Pacific Northwest Research Station
Forestry Sciences Laboratory
3200 SW Jefferson Way
Corvallis, Oregon 97331

Economic Analysis of Forest Landscape Management Alternatives

Bruce R. Lippke, John Sessions, and Andrew B. Carey, 1996, College of Forest Resources, University of Washington ($25.00), CINTRAFOR Special Paper 21 ($25.00)

Recent concern for the ecological impacts of intensive forest management in the Pacific Northwest has resulted in significant federally funded research to evaluate the ecological and economic consequences of forest policy and management. Examples include the Washington State Forest Landscape Management Project (the topic of this report) and the Coastal Landscape Analysis and Modeling Study which focuses on forests in western Oregon. Generally, this research has been interdisciplinary and draws on the expertise of foresters, ecologists, wildlife biologists, and economists. Of particular interest is the evaluation of policy alternatives with which to induce private forest landowners to manage forests for the joint production of timber and nontimber benefits such as habitat for salmon and other endangered species. Reports describing the results of these research efforts are just now emerging.

The Washington State Forest Landscape Management Project was implemented at the request of the U.S. Congress to analyze the economic and ecological consequences of managing forests for both timber production and nontimber values across multiple ownerships. The report discussed in this review *Economic Analysis of Forest Landscape Management Alternatives* focuses on the economic consequences of different biodiversity management alternatives. A second report *A Pragmatic Ecological Approach to Small-landscape Management* (also reviewed in this issue of *Northwest Science*) is intended as a companion to the first and provides an overview of the linkages between habitat and forest structures and the characteristics of biodiversity management.

In *Economic Analysis of Forest Landscape Management Alternatives*, Lippke et al. develop and evaluate financial incentives with which to motivate landowners to include nontimber objectives along with timber objectives in the management of private forest lands. The goal is jointly producing timber and biologically diverse habitat associated with late seral and old-growth forests. This report compares the economic costs and ecological benefits of biodiversity management pathways to the costs and benefits of status quo management which "maximizes the present net worth of forest land owners (p.1)." The analysis develops a set of silvicultural treatments, each resulting in different ecological consequences, timber benefits for the landowner, and regional economic impacts. These impacts are compared to the costs associated with motivating landowners to adopt the set of silvicultural treatments using competitive contracts issued through a public agency or private biodiversity trust purchasers.

The book is organized in eight sections that summarize results in the first four sections; then discuss structuring incentives to increase nonmarket values, regional economic impacts of incentives, and carbon mitigation benefits in the next three sections; and concludes with directions for future research. In the Introduction, biodiversity management pathways are defined by the authors as "special management alternatives designed to create greater diversity in forest structure (p. 2)." These management regimes are characterized by sequential thinning, long rotations (>100 years), and minimum standards regarding snag and downed wood. Section I characterizes financial returns for base line and biodiversity management pathways for a single stand. The analysis focuses on western hemlock on the Olympic Peninsula in Washington, but notes that similar treatments could be developed for other regions. The ecological consequences of following one or another of the biodiversity management pathway are briefly presented in Section II by predicting the resulting stand structure and habitat indices which "act as indicators of the non-timber benefits to compare to the cost associated with lost timber revenue (p. 4)." The habitat indices are described in the companion report, *A Pragmatic Ecological Approach to Small-landscape Management,* along with a more thorough discussion of the biodiversity management pathways. Sections III and IV extend the analysis from the single stand level to the landscape level. Specifically, Section III develops a set of treatment "mixes" that can be weighted across several stands and describes the economic and biodiversity impacts resulting from each. Section IV considers a subset of these treatment mixes using a harvest scheduling model to

simulate the implementation of biodiversity pathways on a 16,000+ acre watershed.

Section V discusses how to structure incentives with which to motivate landowners to manage forests according to the long rotation biodiversity management pathways. These incentives focus on: 1) compensating landowners for increased management costs and decreased timber revenue, 2) landowners' cash flow, 3) reducing risks associated with potential confiscation resulting from endangered species being found in the stand, and 4) the infrastructure necessary to provide needed forest management treatments. The authors focus on competitive contracts with a public agency or trust as incentives to modify landowner management. Sections VII and VIII discuss the economic and other benefits derived from pursuing a program of competitive contracts to motivate longer rotations on private forest land. Specifically, Section VI describes the potential regional economic benefits and Section VII describes the anticipated carbon sequestration benefits. Future research needs are suggested in Section VIII, with six research areas described that center on improving analyses of real environmental and economic trade-offs in land management.

Because the objective of this report is to compare the economic costs and ecological benefits of different management alternatives for conserving biodiversity, readers will find little description of the actual simulation model used to conduct the analysis. The primary landscape simulator is referenced in an unpublished report, which may be costly or not easily obtained by interested readers. A simple schematic showing the model structure accompanied by a brief description in this report would have been useful to readers and perhaps enhanced confidence in the estimates produced. The report does have seven technical appendices, and these provide a thorough description of model assumptions regarding economic data and habitat indices. Economic costs and ecological benefits resulting from following different forest management alternatives are presented in significant detail.

Despite its few short-comings, *Economic Analysis of Forest Landscape Management Alternatives* should contribute to ongoing discourse among researchers and policy-makers regarding forest management and the joint production of timber and nontimber goods and services. The book will be useful to both general and professional readerships, and would be useful in graduate-level resource management courses as a reference document. The book provides a combined view of environmental and economic considerations for managing the Northwest's extensive forests. This multi-disciplinary approach is sometimes missing in separate works from the individual disciplines. Some readers may hope to learn more about what other studies have indicated about actual landowner behavior and whether landowners would be receptive to the types of incentives proposed, including how such incentives stack up against financial returns derived from nonforest use of the land. Such details would require a broader treatment of developed land-use options than provided in this book. The analysis should serve to generate constructive debate among timber and nontimber advocates regarding appropriate forest management in the future. In this respect, simulation models such as the Washington State Forest Landscape Management Project, which simultaneously evaluate the ecological and economic consequences of forest policy and management, may find their greatest value.

—Ralph J. Alig and Jeffrey Kline
Pacific Northwest Research Station
Forestry Sciences Laboratory
3200 SW Jefferson Way
Corvallis, Oregon 97331

Northwest Science
Volume 71 (1997)
Author and Subject Index

AUTHOR entry headings are distinguished from subject entry headings by capitalization.

ADKISON, M.D. *see* Berg et al., 305-312
AGEE, J.K. NWS Forum: The severe weather wildfire—too hot to handle? 153-156
air quality
  nitrogen dioxide monitoring, Bruce and Gow, 330-339
Alaska
  asymmetry in male sockeye salmon, Berg et al., 305-312
AMES, K.A. Book Review: *The Hoko River Archaeological Site Complex* (Croes). 72-74
AMSBERRY, K.A. *see* McCune et al., 145-152
ants
  thatch ant supercolony, McIver et al., 18-29
archaeology
  Hoko River site (book review), Ames, 72-74
  prehistory of Beringia (book review), Carlson, 165-166

BACIGALUPI, M. *see* Bingham et al., 108-114
BERG, O.K., M.D. ADKISON, and T.P. QUINN. Bilateral asymmetry, sexual dimorphism, and nematode parasites in mature male sockeye salmon *Oncorhynchus nerka*. 305-312
BINGHAM, B.L., M. BACIGALUPI, and L.G. JOHNSON. Temperature adaptations of embryos from intertidal and subtidal sand dollars (*Dendraster excentricus*, Eschscholtz). 108-114
birds
  bald eagles in Washington, Stalmaster and Kaiser, 214-223
  effects of silvicultural treatments, Chambers and McComb, 298-304
  forest breeding bird surveys in Washington, Bosakowski, 244-253 (corrected version)
  riparian reserve zone birds, Kinley and Newhouse, 75-86
BOLTE, J. Book Review: *Building Knowledge-based Systems for Natural Resource Management* (Schmoldt and Rauscher). 340-341
book reviews
  American Beginnings: The Prehistory and Paleoecology of Beringia (West), Carlson, 165-166
  Building Knowledge-based Systems for Natural Resource Management (Schmoldt and Rauscher), Bolte, 340-341
  Clean Water: The Citizen's Complete Guide to Water Quality and Water Pollution Control (Vigil), Major, 161-162
  Creating a Forestry for the 21st Century. The Science of Ecosystem Management (Kohm and Franklin), Boyle, 350-352
  Do Lemmings Commit Suicide? Beautiful Hypotheses and Ugly Facts (Chitty), Ydenberg, 163-164
  Foundations of Animal Behavior: Classic Papers with Commentaries (Houck and Drickamer), Lank, 346-347
  Lost Landscapes and Failed Economies—The Search for a Value of Place (Power), Landers, 159-160
  Metapopulations and Wildlife Conservation (McCullough), Wolff's class, 258-259
  Phylogenies and the Comparative Method in Animal Behavior (Martins), Verrell, 344-345
  Principles and Practice of Plant Conservation (Given), Manasse, 68-69
  Restoring Diversity: Strategies for Reintroduction of Endangered Plants (Falk et al.), Liston, 70-71
  Rights to Nature: Ecological, Economic, Cultural, and Political Principles of Institutions for the Environment (Hanna et al.), White, 157-158
  The Ecological Detective: Confronting Models with Data (Hilborn and Mangel), Van Sickle, 342-343
  The Hoko River Archaeological Site Complex (Croes), Ames, 72-74
  The Northwest Salmon Crisis: A Documentary History (Cone and Ridlington), Hanna, 66-67
  The Rain Forests of Home: Profile of a North American Bioregion (Schoonmaker et al.), Solomon, 348-349
BOSAKOWSKI, T. Breeding bird abundance and habitat relationships on a private industrial forest in the western Washington Cascades. 244-253 (corrected version)
botany
  Corydalis aquae-gelidae, Goldenberg and Zobel, 196-204
  genetic diversity in bulbous bluegrass, Novak and Welfley, 271-280
  glutathione reductase in lodgepole pine, Harris and Dalton, 205-213
  plant conservation (book review), Manasse, 68-69
  reintroducing endangered plants (book review), Liston, 70-71
BOYLE, J.R. Book Review: *Creating a Forestry for the 21st Century. The Science of Ecosystem Management* (Kohm and Franklin). 350-352
British Columbia
  atmospheric nitrogen dioxide monitoring, Bruce and Gow, 330-339
  birds in riparian reserve zones, Kinley and Newhouse, 75-86
  forest herbicides and small mammals, Sullivan et al., 6-17
  Pacific yew growth and propagation, Mitchell, 56-63
  western redcedar site index, Kayahara et al., 167-173
BRUCE, G.R., and T.A. GOW. Patterns of atmospheric nitrogen dioxide in Kelowna, British Columbia. 330-339

California
  northern flying squirrel diets, Zabel and Waters, 103-107
CAMACHO, F.J. *see* McCune et al., 145-152
CARLSON, R.L. Book Review: *American Beginnings* (West). 165-166
CASE, R.L., and J.B. KAUFFMAN. Wild ungulate influences on the recovery of willows, black cottonwood and thinleaf alder following cessation of cattle grazing in northeastern Oregon. 115-126

CHAMBERS, C.L., and W.C. McCOMB. Effects of silvicultural treatments on wintering bird communities in the Oregon Coast Range. 298-304
CIMON, N.J. *see* McIver et al, 18-29
CLERY, S. *see* McCune et al., 145-152
COBLENTZ, B.E. *see* Payer and Coblentz, 281-288
COLE, C. *see* McCune et al., 145-152
conservation
  metapopulations and wildlife conservation (book review), Wolff's class, 258-259
  plant conservation (book review), Manasse, 68-69
  reintroducing endangered plants (book review), Liston, 70-71
coyotes
  food habits, Quinn, 1-5
  habitat selection, Quinn, 289-297

DALTON, D.A. *see* Harris and Dalton, 205-213
DEEGAN, L.A. *see* Gettel et al., 224-232
deer
  role of wild ungulates in riparian recovery, Case and Kauffman, 115-126
DEIMLING, E.K. *see* Gresswell et al., 39-44

echinoderms
  sand dollar temperature adaptations, Bingham et al., 108-114
ecology
  biological monitoring and water quality, Karr, 254-257
  economics of natural resources (book review), Landers, 159-160
  environmental policy (book review), White, 157-158
  forestry for the 21st century (book review), Boyle, 350-352
  models and data (book review), Van Sickle, 342-343
  plant conservation (book review), Manasse, 68-69
  reintroducing endangered plants (book review), Liston, 70-71
  rodent population fluctuations (book review), Ydenberg, 163-164
  role of wild ungulates in riparian recovery, Case and Kauffman, 115-126
  salmon crisis in Northwest (book review), Hanna, 66-67
  vertical profile in old-growth forest, McCune et al., 145-152
  western redcedar site index, Kayahara et al., 167-173
elk
  effect on cottonwood in Yellowstone, Keigley, 127-136
  role of wild ungulates in riparian recovery, Case and Kauffman, 115-126
EMERSON, C. *see* McCune et al., 145-152
EMMETT, R.L. *see* McCabe et al., 45-55
environmental policy
  rights to nature (book review), White, 157-158
epiphytes
  commercial moss harvest, Peck, 186-195
  vertical profile in old-growth forest, McCune et al., 145-152
ethology
  foundations of animal behavior (book review), Lank, 346-347
  phylogenies and animal behavior (book review), Verrell, 344-345

FELDER, G. *see* McCune et al., 145-152
FILIP, G.M., and L. YANG-ERVE. Effects of prescribed burning on the viability of *Armillaria ostoyae* in mixed-conifer forest soils in the Blue Mountains of Oregon. 137-144
fires
  combustion propagation, Jones, 64-66
  effects of multiple forest fires, Gray and Franklin, 174-185
  prescribed burning and *Armillaria ostoyae*, Filip and Yang-Erve, 137-144
  wildfires and weather, Agee, 153-156
fish
  Arctic grayling otoliths, Gettel et al., 224-232
  asymmetry in male sockeye salmon, Berg et al., 305-312
  bull trout in Clark Fork River, Swanberg, 313-317
  cutthroat trout otoliths and scales, Kruse et al., 30-38
  estimating fish abundance, Gresswell et al., 39-44
  salmon crisis in Northwest (book review), Hanna, 66-67
forests
  birds in riparian reserve zones, Kinley and Newhouse, 75-86
  breeding bird surveys in Washington forest, Bosakowski, 244-253 (corrected version)
  commercial moss harvest, Peck, 186-195
  Corydalis aquae-gelidae, Goldenberg and Zobel, 196-204
  effects of multiple forest fires, Gray and Franklin, 174-185
  epiphytes in old-growth forest, McCune et al., 145-152
  forestry for the 21st century (book review), Boyle, 350-352
  glutathione reductase in lodgepole pine, Harris and Dalton, 205-213
  herbicides and small mammals, Sullivan et al., 6-17
  northern flying squirrel diets, Rosentreter et al., 97-102
  northern flying squirrel food preferences, Zabel and Waters, 103-107
  old-growth canopy light, Parker, 261-270
  Pacific yew growth and propagation, Mitchell, 56-63
  prescribed burning and *Armillaria ostoyae*, Filip and Yang-Erve, 137-144
  rain forests of North America (book review), Solomon, 348-349
  sediment loading model evaluation, Hickey, 233-242
  silvicultural treatments and birds, Chambers and McComb, 298-304
  thatch ant supercolony, McIver et al., 18-29
  western redcedar site index, Kayahara et al., 167-173
FOSBERG M.A. *see* Othberg et al., 318-329
FRANKLIN, J.F. *see* Gray and Franklin, 174-185
FRENCH, P. *see* McCune et al., 145-152
fungi
  prescribed burning and *Armillaria ostoyae*, Filip and Yang-Erve, 137-144

geology
  terrace soils of Boise valley, Othberg et al., 318-329
GETTEL, G.M., L.A. DEEGAN, and C.J. HARVEY. A comparison of whole and thin-sectioned otolith aging techniques and validation of annuli for Arctic grayling. 224-232
GOLDENBERG, D.M., and D.B. ZOBEL. Allocation, growth and estimated population structure of *Corydalis aquae-gelidae*, a rare riparian plant. 196-204
GOW, T.A. *see* Bruce and Gow, 330-339

GRAY, A.N., and J.F. FRANKLIN. Effects of multiple fires on the structure of southwestern Washington forests. 174-185
GREENE, D. *see* McCune et al., 145-152
GRESSWELL, R.E., W.J. LISS, G.A. LOMNICKY, E.K. DEIMLING, R.L. HOFFMAN, and T. TYLER. Using mark-recapture methods to estimate fish abundance in small mountain lakes. 39-44

HANNA, S.S. Book Review: *The Northwest Salmon Crisis* (Cone and Ridlington). 66-67
HARRIS, R. *see* McCune et al., 145-152
HARRIS, W.N., and D.A. DALTON. Seasonal variation in glutathione reductase activity in coastal and montane populations of lodgepole pine (*Pinus contorta*). 205-213
HARVEY, C.J. *see* Gettel et al., 224-232
HAYWARD, G.D. *see* Rosentreter et al., 97-102
herbicides
  glyphosate herbicide and small mammals, Sullivan et al., 6-17
HICKEY, R. Evaluating the WATBAL sediment loading model, Clearwater National Forest, Idaho. 233-242
HINTON, S.A. *see* McCabe et al., 45-55
HOFFMAN, R.L. *see* Gresswell et al., 39-44
Hoko River
  archaeological site (book review), Ames, 72-74
HUBERT, W.A. *see* Kruse et al., 30-38
HUTTEN, M. *see* McCune et al., 145-152

Idaho
  northern flying squirrel diets, Rosentreter et al., 97-102
  sediment loading model evaluation, Hickey, 233-242
  terrace soils of Boise valley, Othberg et al., 318-329
invertebrates
  benthic invertebrates in Columbia River, McCabe et al., 45-55
  sand dollar temperature adaptations, Bingham et al., 108-114
  thatch ant supercolony, McIver et al., 18-29

JOHNSON, L.G. *see* Bingham et al., 108-114
JONES, J.C. NWS Forum: Deliberations on smoldering propagation of combustion in groundlayers of humic substances. 64-65

KAISER, J.L. *see* Stalmaster and Kaiser, 214-223
KARR, J.R. NWS Forum: The future is now: biological monitoring to ensure healthy waters. 254-257
KAUFFMAN, J.B. *see* Case and Kauffman, 115-126
KAYAHARA, G.J., K. KLINKA, and A.C. SCHROFF. The relationship of site index to synoptic estimates of soil moisture and nutrients for western redcedar (*Thuja plicata*) in southern coastal British Columbia. 167-173
KEIGLEY, R.B. An increase in herbivory of cottonwood in Yellowstone National Park. 127-136
KINLEY, T.A. and N.J. NEWHOUSE. Relationship of riparian reserve zone width to bird density and diversity in southeastern British Columbia. 75-86
KLINKA, K. *see* Kayahara et al., 167-173
KRUSE, C.G., W.A. HUBERT, and F.J. RAHEL. Using otoliths and scales to describe age and growth of Yellowstone cutthroat trout in a high-elevation stream system, Wyoming. 30-38

lakes
  estimating fish abundance, Gresswell et al., 39-44
LANDERS, D.H. Book Review: *Lost Landscapes and Failed Economies* (Power). 159-160
LANK, D.B. Book Review: *Foundations of Animal Behavior: Classic Papers with Commentaries* (Houck and Drickamer). 346-347
LARSON, B. *see* McCune et al., 145-152
LAUTENSCHLAGER, R.A. *see* Sullivan et al., 6-17
LESKO, M. *see* McCune et al., 145-152
LISS, W.J. *see* Gresswell et al., 39-44
LISTON, A. Book Review: *Restoring Diversity: Strategies for Reintroduction of Endangered Plants* (Falk et al.). 70-71
LOMNICKY, G.A. *see* Gresswell et al., 39-44

MAJOR, J.J. Book Review: *Clean Water* (Vigil). 161-162
MAJORS, S. *see* McCune et al., 145-152
mammals, large
  bighorn ram habitat use, Payer and Coblentz, 281-288
  coyote diets, Quinn, 1-5
  coyote habitat selection, Quinn, 289-297
  elk and cottonwood in Yellowstone, Keigley, 127-136
  role of wild ungulates in riparian recovery, Case and Kauffman, 115-126
mammals, small
  effects of forest herbicides, Sullivan et al., 6-17
  northern flying squirrel diets, Rosentreter et al., 97-102
  northern flying squirrel food preferences, Zabel and Waters, 103-107
  rodent population fluctuations (book review), Ydenberg, 163-164
MANASSE, R.S. Book Review: *Principles and Practice of Plant Conservation* (Given). 68-69
MARKWELL, T. *see* McCune et al., 145-152
McCABE, G.T. Jn., S.A. HINTON, R.L. EMMETT, and B.P. SANDFORD. Benthic invertebrates and sediment characteristics in main channel habitats in the lower Columbia River. 45-55
McCOMB, W.C. *see* Chambers and McComb, 298-304
McCUNE, B., K.A. AMSBERRY, F.J. CAMACHO, S. CLERY, C. COLE, C. EMERSON, G. FELDER, P. FRENCH, D. GREENE, R. HARRIS, M. HUTTEN, B. LARSON, M. LESKO, S. MAJORS, T. MARKWELL, G.G. PARKER, K. PENDERGRASS, E.B. PETERSON, E.T. PETERSON, J. PLATT, J. PROCTOR, T. RAMBO, A. ROSSO, D. SHAW, R. TURNER, and M. WIDMER. Vertical profile of epiphytes in a Pacific Northwest old-growth forest. 145-152
McDANIEL, P.A. *see* Othberg et al., 318-329
McIVER, J.D., T.R. TORGERSEN, and N.J. CIMON. A supercolony of the thatch ant *Formica obscuripes* Forel (Hymenoptera: Formicidae) from the Blue Mountains of Oregon. 18-29
MITCHELL, A.K. Propagation and growth of Pacific yew (*Taxus brevifolia* Nutt.) cuttings. 56-63
Montana
  bull trout in Clark Fork River, Swanberg, 313-317
mosses
  commercial moss harvest, Peck, 186-195

NEWHOUSE, N.J. *see* Kinley and Newhouse, 75-86
NOVAK, S.J., and A.Y. WELFLEY. Genetic diversity in the introduced clonal grass *Poa bulbosa* (bulbous bluegrass). 271-280
NWS Forum
  biological monitoring for healthy water, Karr, 254-257
  combustion propagation, Jones, 64-65
  wildfires and weather, Agee, 153-156

Oregon
  bighorn ram habitat use, Payer and Coblentz, 281-288
  commercial moss harvest, Peck, 186-195
  prescribed burning and *Armillaria ostoyae*, Filip and Yang-Erve, 137-144
  role of wild ungulates in riparian recovery, Case and Kauffman, 115-126
  silvicultural treatments and birds, Chambers and McComb, 298-304
  thatch ant supercolony, McIver et al., 18-29
OTHBERG, K.L., P.A. McDANIEL, and M.A. FOSBERG. Soil development on a Pleistocene terrace sequence, Boise Valley, Idaho. 318-329

PARKER, G.G. Canopy structure and light environment of an old-growth Douglas-fir/western hemlock forest. 261-270
———— *see* McCune et al., 145-152
PAYER, D.C., and B.E. COBLENTZ. Seasonal variation in California bighorn ram (*Ovis canadensis californiana*) habitat use and group size. 281-288
PECK, J.E. Commercial moss harvest in northwestern Oregon: describing the epiphyte communities. 186-195
PENDERGRASS, K. *see* McCune et al., 145-152
PETERSON, E.B. *see* McCune et al., 145-152
PETERSON, E.T. *see* McCune et al., 145-152
PLATT, J. *see* McCune et al., 145-152
PROCTOR, J. *see* McCune et al., 145-152

QUINN, T. Coyote (*Canis latrans*) food habits in three urban habitat types of western Washington. 1-5
———— Coyote (*Canis latrans*) habitat selection in urban areas of western Washington via analysis of routine movements. 289-297
QUINN, T.P. *see* Berg et al., 305-312

RAHEL, F.J. *see* Kruse et al., 30-38
RAMBO, T. *see* McCune et al., 145-152
resource management
  natural resource management (book review), Bolte, 340-341
rivers
  benthic invertebrates in Columbia River, McCabe et al., 45-55
  bull trout in Clark Fork River, Swanberg, 313-317
rodents
  population fluctuations (book review), Ydenberg, 163-164
ROSENTRETER, R., G.D. HAYWARD, and M. WICKLOW-HOWARD. Northern flying squirrel seasonal food habits in the interior conifer forests of central Idaho, USA. 97-102
ROSSO, A. *see* McCune et al., 145-152

SANDFORD, B.P. *see* McCabe et al., 45-55
SCHROFF, A.C. *see* Kayahara et al., 167-173
SHAW, D. *see* McCune et al., 145-152
sheep
  bighorn ram habitat use, Payer and Coblentz, 281-288
soils
  terrace soils of Boise valley, Othberg et al., 318-329
SOLOMON, A.M. Book Review: *The Rain Forests of Home: Profile of a North American Bioregion* (Schoonmaker et al.). 348-349
squirrels
  northern flying squirrel diets, Rosentreter et al., 97-102
  northern flying squirrel food preferences, Zabel and Waters, 103-107
STALMASTER, M.V., and J.L. KAISER. Winter ecology of bald eagles in the Nisqually River drainage, Washington. 214-223
streams
  birds in riparian reserve zones, Kinley and Newhouse, 75-86
  cutthroat trout otoliths and scales, Kruse et al., 30-38
  role of wild ungulates in riparian recovery, Case and Kauffman, 115-126
  sediment loading model evaluation, Hickey, 233-242
SULLIVAN, D.S. *see* Sullivan et al., 6-17
SULLIVAN, T.P., D.S. SULLIVAN, R.A. LAUTENSCHLAGER, and R.G. WAGNER. Long-term influence of glyphosate herbicide on demography and diversity of small mammal communities in coastal coniferous forest. 6-17
SWANBERG, T.R. Movements of bull trout (*Salvelinus confluentus*) in the Clark Fork River system after transport upstream of Milltown Dam. 313-317

TORGERSEN, T.R. *see* McIver et al, 18-29
TURNER, R. *see* McCune et al., 145-152
TYLER, T. *see* Gresswell et al., 39-44

ungulates
  elk and cottonwood in Yellowstone, Keigley, 127-136
  role in riparian degradation and recovery, Case and Kauffman, 115-126

VAN SICKLE, J. Book Review: *The Ecological Detective: Confronting Models with Data* (Hilborn and Mangel). 342-343
VERRELL, P.A. Book Review: *Phylogenies and the Comparative Method in Animal Behavior* (Martins). 344-345

WAGNER, R.G. *see* Sullivan et al., 6-17
Washington
  bald eagles in Nisqually River drainage, Stalmaster and Kaiser, 214-223
  breeding forest bird surveys, Bosakowski, 244-253 (corrected version)
  coyote diets, Quinn, 1-5
  coyote habitat selection, Quinn, 289-297
  effects of multiple forest fires, Gray and Franklin, 174-185
  old-growth forest canopy light, Parker, 261-270
  sand dollar temperature adaptations, Bingham et al., 108-114
  vertical profile of epiphytes in old-growth forest, McCune et al., 145-152
water quality
  biological monitoring, Karr, 254-257
  clean water (book review), Major, 161-162
  sediment loading model evaluation, Hickey, 233-242
WATERS, J.R. *see* Zabel and Waters, 103-107

weather
wildfires and weather, Agee, 153-156
WELFLEY, A.Y. *see* Novak and Welfley, 271-280
WHITE, D. Book Review: *Rights to Nature* (Hanna et al.). 157-158
WICKLOW-HOWARD, M. *see* Rosentreter et al., 97-102
WIDMER, M. *see* McCune et al., 145-152
WOLFF, J.O. Book Review by his class: *Metapopulations and Wildlife Conservation* (McCullough). 258-259
Wyoming
cutthroat trout otoliths and scales, Kruse et al., 30-38
elk and cottonwood, Keigley, 127-136

YANG-ERVE, L. *see* Filip and Yang-Erve, 137-144
YDENBERG, R. Book Review: *Do Lemmings Commit Suicide* (Chitty). 163-164
Yellowstone National Park
elk and cottonwood, Keigley, 127-136

ZABEL, C.J., and J.R. WATERS. Food preferences of captive northern flying squirrels from the Lassen National Forest in northeastern California. 103-107
ZOBEL, D.B. *see* Goldenberg and Zobel, 196-204

NORTHWEST SCIENCE

Information for Authors

Scope of Articles

The pages of *Northwest Science* are open to original and fundamental research in the basic, applied, and social sciences. *Northwest Science* does not generally publish notes or review articles. All submissions are refereed, usually by two reviewers. Papers are welcome from authors outside of the Pacific Northwest, but at least one author of any paper considered for publication must be a member of the Northwest Scientific Association.

Manuscripts

General Instructions: Submit four copies of the paper (including tables and figures) to the Editor. Manuscripts should be typewritten on 8-1/2 x 11 inch paper, double-spaced throughout (including abstract, acknowledgments, literature cited, tables, and legends for figures); ample margins must also be provided. Unnecessary footnotes should be avoided.

The manuscript should consist of sections in the following sequence:

- Title Page
- Abstract
- Text (Introduction through Acknowledgments)
- Literature Cited
- Footnotes
- Tables
- Figure Legends
- Figures

Maximum article length for papers published in *Northwest Science* is 16 journal pages. Two typed pages are approximately equal to one journal page.

Numerals will be used to indicate footnotes unless such usage would be confused with numerical data. In this situation, lowercase letters should be used. Do not break, or hyphenate, words at the ends of lines. Words to be italicized should be typed in italics.

The format and style of manuscripts should conform to general usage in recent issues.

Title Page: The first page of the manuscript should contain:

- Author's name (or names)
- Institutional address from which manuscript emanated, including city, state or province, postal code
- Title of paper
- Running head
- Total number of text figures and tables
- *Correspondence to:* List name, full address, telephone number, fax number, and e-mail address of the individual to whom correspondence should be sent.

Abstract: The purpose of an abstract is to briefly summarize the study so it is quickly accessible to the general readership of the journal. The abstract, written in complete sentences and not exceeding 250 words, should precede the text on a separate page. Authors are reminded of the diverse disciplines and readership served by the journal. With this in mind the abstract should have three parts of unequal length. First, the abstract should begin with a statement of the purpose of the study that indicates *why the study was undertaken.* Next the experimental design or approach should be stated and the *results summarized.* The abstract should end with a sentence or two on the larger significance of the research. Authors are strongly encouraged to give the abstract proper attention.

Text: Literature citations within the manuscript text should contain the author's name and year of publication, using formats A and B.

- Format A:
  ...studied by Jones (1978)...
  ...studied by Smith and Brown (1979)...
  ...studied by Smith et al. (1980)... (if more than two authors in a citation)
- Format B:
  ...was previously investigated (Smith 1965, Jones 1971, Harris 1982)...

...results of other investigations (Smith 1966, 1970; Jones 1973; Brown 1974)...

Numbers from one to nine will be spelled out, while arabic numerals will be used for numbers 10 and larger. Exceptions to this rule are: 1) a series of "mixed" numbers (e.g., 14 elk, 35 deer, 2 bobcats, and 1 bear); 2) when the number immediately precedes an abbreviation for a standard unit of measure (e.g., 3 g, 18 mm, 300 m^2). Numerals will also be used for dates, times, page numbers, and percentages.

Present all data in international (SI) unites. English equivalents may be added parenthetically. Use the 24-hour clock (0600 and 2230) and continental dating (17 November 1986).

On first mention, a species should be designated by common name followed by systematic binomial (italicized). Common names for species should not be capitalized except when derived from a proper name. Thus, "mountain hemlock" or "white-crowned sparrow," but "Douglas-fir" or "Clark's nutcracker." For abbreviations and forms of titles for serial publications, follow the BIOSIS List of Serials. Consult with the Council of Biology Editors *CBE Style Manual,* 4th ed., for general information on manuscript preparation.

Literature Cited: Only the *first letter* of the *first word* of journal articles, technical reports, theses, etc. are capitalized. First letters of *major words* in book titles are capitalized. All authors of a title are listed in the bibliographic citation ("et al." is used only in the body of the text).

Citation of unpublished reports is discouraged. Rather, cite the sources as a personal communication from the senior author (P. W. Smith pers. comm.).

Citations should be double-spaced and listed in alphabetical order at the end of the article. Listed below are some typical citations.

Journal articles

Broadbooks, H. E. 1970a. Home range and territorial behavior of the yellow pine chipmunk *Eutamius amoenus.* J. Mammal. 51:310-326.

_____. 1970b. Populations of the yellow pine chipmunk, *Eutamius amoenus.* Amer. Midl. Nat. 83:472-488.

Ceska, A., and H. Romer. 1971. A computer program for identifying species group. Vegetatio 20:48-73.

Grizze, J. E., C. F. Starmer, and G. G. Kuch. 1969. Analysis of categorical data by linear models. Biometrics 25:489-504.

Monographs or books

Jennings, H. S. 1906. Behavior of the Lower Organisms. Columbia University Press, New York.

Papers in proceedings or symposia

Ryland, J. S. 1975. Parameters of the lophophore in relation to population structure in a bryozoan community. *In* H. Barnes (ed.) Proc. 9th Eur. Mar. Biol. Symp., Aberdeen University Press, Aberdeen. Pp. 363-393.

Theses, dissertations, personal communications, and articles in press

Donald, D. B. 1971. The limnology of the plankton of three temporary pons in Alberta. University of Calgary, Calgary. M.S. Thesis.

Wiser, H. C. 1961. Decomposition and homogeneity of continua on 2-manifolds. University of Utah, Salt Lake City. Ph.D. Dissertation.

Danwiddie, P. W. In Press. Dichotomous key to conifer foliage in the Pacific Northwest. Northw. Sci.

Technical Bulletins

Daubenmire, R., and J. B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. Wash. Agric. Exp. Sta. Tech. Bull. 60. Washington State University. 210 p.

Goodwin, J. G., Jr., and C. R. Hungerford. 1979. Rodent population densities in pine forests. USDA For. Serv. Res. Pap. RM-214. Rocky Mtn. For. Range Exp. Sta., Fort Collins, Colorado. 39 p.

Footnotes: Footnotes to the text should be limited as much as possible and must be numbered consecutively. The corresponding numbers must be clearly indicated in the text.

Tables: All tables must be cited in the text, but typewritten (double-spaced) on separate pages. When submitting tables electronically, they should be presented in the simplest tabular format possible, and placed in a separate file from text.

Figures: All figures must be cited in the text. To achieve greater published fidelity, it is preferable for the printer to work directly from original photographs or drawings. Thus, original artwork or black & white glossy prints of photographs must be submitted for reproduction. When sent, be sure to include enough firm backing (e.g., lettering board) to protect them from damage. Artwork and lettering should be large enough (but not overly large) to provide clarity after a 50% reduction in size for printing. *The author's name and figure number should be penciled on the back of each illustration.* Provide a scale for distance

on map illustrations. Legends for illustrations should be typed as a group and placed on a separate page. In reference to figures and tables the words "Figure" and "Table" should be spelled out and capitalized as follows:

- ...experimental sites as indicated in Figure 2...
- ...correlation between temperature and biomass (Table 3)...

Artwork, photography, and camera ready art cannot be returned to the author.

Editing—The Editor reserves the right to edit manuscripts for grammatical correctness and clarity.

Submission of Final Copy—Manuscripts accepted for publication must be submitted in electronic copy as well as hard copy. Authors will receive instructions from the Editor regarding acceptable word processing software.

Publication Agreement—Each author or group of authors must sign a Publication Agreement provided by the Editor before their submission will be published in the journal.

Galley Proofs and Reprints—One set of proofs will be sent to the indicated author for correction shortly before publication; proofs should be returned to the Editor within *three days* of receipt. Authors should inform the Editor of any change of address for handling proofs. Reprints must be ordered when the proofs are returned. A schedule of reprint prices will be sent to the author with the proofs. Allow 8 weeks for delivery after the journal issue carrying the article appears.

Page Charges—Page charges are currently $60 per printed page. A bank draft, money order, or institutional purchase order to cover page charges and optional reprints should be submitted to the Editor upon return of galley proofs.

Correspondence—All correspondence regarding manuscripts will be between the corresponding author and Editor.

Reviewers—The associate editors reserve the right to select reviewers of their choice.

WSU PRESS Washington State University Press
PO Box 645910
Pullman, Washington 99164-5910 USA

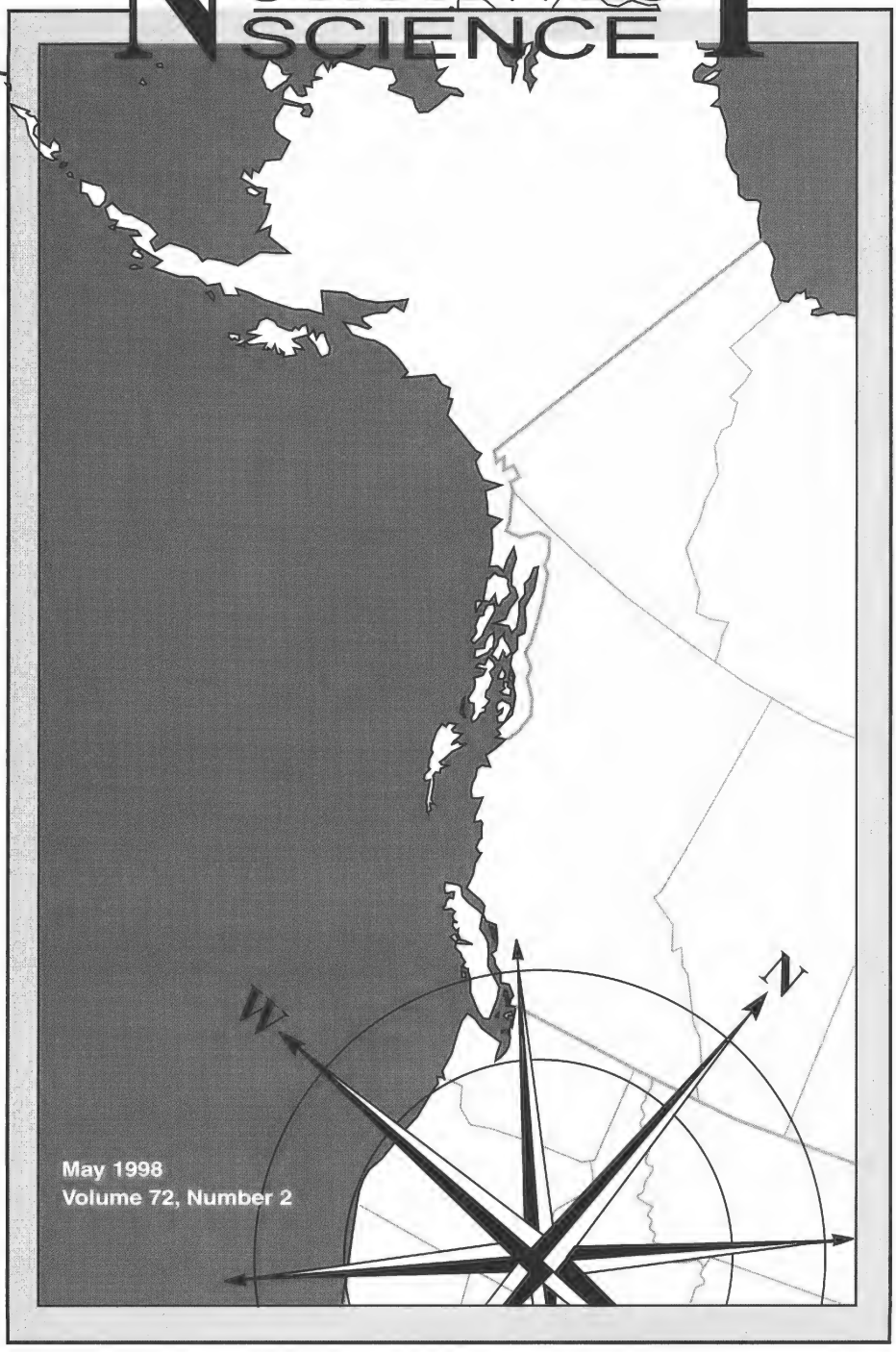
Nonprofit Organization
U.S. Postage
PAID
Pullman, WA
Permit No. 1

Northwest Science

Quarterly Publication of the Northwest Scientific Association

Papers published in **Northwest Science** are indexed in *Current Contents, Science Citation Index, Biological Abstracts, The Zoological Record, Recent Literature Supplement to The Auk, Abstracts in Anthropology, Bibliography and Index of Geology, Chemical Abstracts, Bibliography of Agriculture, Forestry Abstracts, University Microfilms, Geo Abstracts, GEOBASE,* and *Cambridge Scientific Abstracts.*

NORTHWEST SCIENCE



May 1998
Volume 72, Number 2

Northwest Scientific Association

(Founded 1923)

The Northwest Scientific Association, an affiliate of the American Association for the Advancement of Science, is an association representative of the basic and applied sciences and of social sciences.

Membership in the Northwest Scientific Association, which includes a subscription to *Northwest Science,* is open to individuals for $25 per year ($10 per year for students). Institutional membership, $40 per year. Sustaining membership, $40 per year for individuals and $100 per year for organizations, institutions, or agencies. Subscriptions are for the calendar year only.

Send membership dues, changes of address, and requests for undelivered issues to the Treasurer.

The Northwest Scientific Association is a 501-C(3) tax status organization.

Editor of *Northwest Science*

Edward G. Schreiner
USGS/BRD, Olympic Field Station
600 E Park Avenue
Port Angeles, Washington 98362
Telephone: 360-452-4501 x244
Fax: 360-452-0335
Internet: Ed_Schreiner@nps.gov

Officers of the Association

President Theodore B. Thomas
USDI Fish & Wildlife Service
Olympia, Washington (2000)*

Past President Richard Cellarius
The Evergreen State College
Olympia, Washington

Secretary Margaret O'Connell (1999)
Department of Biology MS-72
Eastern Washington University
Cheney, Washington 99004

Treasurer David H. Hansen
Department of Biology
Pacific Lutheran University
Tacoma, Washington 98447 (1997)
Telephone: 206-535-7565
Fax: 206-536-5055
Internet: hansendh@plu.edu

Book Review Editor
Jerry O. Wolff
U.S. Environmental Protection Agency
200 SW 35th Street
Corvallis, Oregon 97333
Telephone: 541-754-4377, Fax: 541-754-4338
e-mail: wolffj@ccmail.orst.edu

Trustees:

Ross Black
Eastern Washington University
Cheney, Washington (1998)

Leonard Broberg
University of Montana
Missoula, Montana (2001)

Sally Hacker
Washington State University
Vancouver, Washington (2001)

Charles Halpern
University of Washington
Seattle, Washington (2000)

Miles Hemstrom
USDA Forest Service
Portland, Oregon (1999)

Kenneth V. Kardong
Washington State University
Pullman, Washington (2001)

Barry L. Keller
Idaho State University
Pocatello, Idaho (1999)

John Koprowski
Willamette University
Salem, Oregon (2000)

Paul A. McDaniel
University of Idaho
Moscow, Idaho (2000)

Kurt Othberg
Idaho Geological Survey
Moscow, Idaho (2000)

Michael D. Pitt
University of British Columbia
Vancouver, British Columbia (1998)

Tim Reynolds
Environmental Science and Research Foundation
Idaho Falls, Idaho (2000)

Roger Rosentreter
Bureau of Land Management
Boise, Idaho (1999)

Steve Sillett
Humboldt State University
Arcata, California (2001)

Darlene Zabowski
University of Washington
Seattle, Washinton (2001)

*Term of office expires in the year given in parentheses.

© 1998 by the Northwest Scientific Association. All rights reserved.

May 1998 Volume 72, Number 2

NORTHWEST SCIENCE

Editor	Edward G. Schreiner	USGS/BRD—Olympic Field Station, Port Angeles
Managing Editor	Nancy J. Grunewald	Washington State University
Indexer	Caroline Hooper	
Associate Editors		
Anthropology	R. Lee Lyman	University of Missouri—Columbia
Aquatic Biology	Gary L. Larson	U.S. Geological Survey—Corvallis
Botany	Eldon H. Franz	Washington State University
Mathematics & Computer Applications	Steven J. Ghan	Battelle Pacific Northwest Labs—Richland
Forestry	Michael C. Feller	University of British Columbia
Geology & Geography	David R. Gaylord	Washington State University
Soils	Robert L. Edmonds	University of Washington
Wildlife Biology	Patricia J. Heglund	University of Idaho
Zoology	Richard B. Forbes	Portland State University
Book Reviews	Jerry O. Wolff	U.S. EPA—Corvallis

ISSN #0029-344X

CONTENTS

Announcements

81 Reconstructing Temperature from Tree Rings of Pacific Silver Fir in Coastal British Columbia—**Jaroslav Dobrý and Karel Klinka**

88 Forest Floor and Soil Nutrients Five Years after Urea Fertilization in a Grand Fir Forest—**A. R. Tiedemann, R. R. Mason and B. E. Wickman**

96 Distribution of the Marbled Murrelet in Southwestern Oregon—**Joseph W. Witt**

102 Habitat Classification Models for Beaver (*Castor canadensis*) in the Streams of the Central Oregon Coast Range—**Nobuya Suzuki and William C. McComb**

111 Biogeographic Analysis of the Coeur d'Alene Salamander (*Plethodon idahoensis*)—**Albert G. Wilson, Jr. and John H. Larsen, Jr.**

116 Benthic Invertebrates and Sediment Characteristics in a Shallow Navigation Channel of the Lower Columbia River, Before and After Dredging—**George T. McCabe, Jr., Susan A. Hinton and Robert L. Emmett**

127 Shore Flies (Diptera: Ephydridae) of the Hanford Site, Washington—**Richard S. Zack**

Northwest Science Forum

142 Aboriginal Whaling—Biological Diversity Meets Cultural Diversity—**Jennifer Sepez Aradanas**

Book Reviews

146 *The Science of Conservation Planning—Habitat Conservation under the Endangered Species Act* by Reed F. Noss, Michael A. O'Connell and Dennis D. Murphy—**reviewed by Eric K. Cole**

148 *Northwest Birds in Winter* by Alan Contreras—**reviewed by Matthew G. Hunter**

150 *Atlas of Oregon Wildlife—Distribution, Habitat, and Natural History* by Blair Csuti, A. Jon Kimerling, Thomas A. O'Neil, Margaret M. Shaughnessy, Eleanor P. Gains and Manuela M. P. Huso—**reviewed by John P. Hayes**

152 *Sea-Run Cutthroat Trout* by James D. Hall, Peter A. Bisson, and Robert E. Gresswell (editors)—**reviewed by Jeff Cederholm**

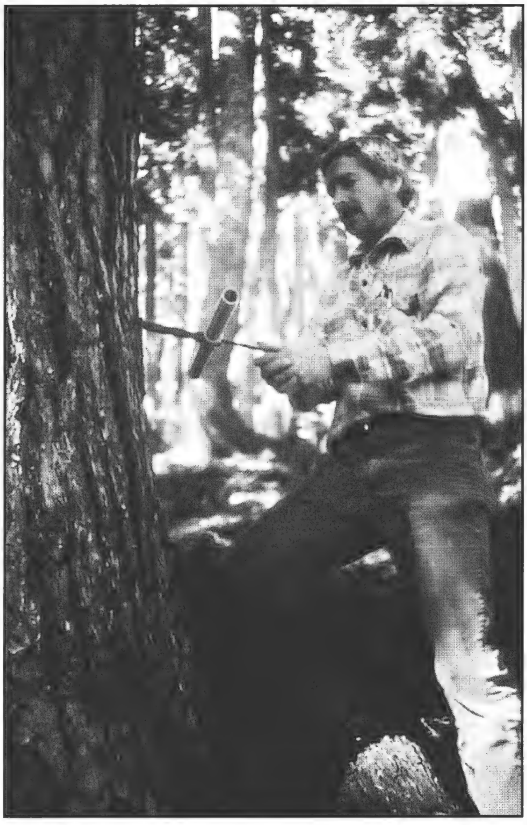
154 *EcoHomo: How the Human Being Emerged from the Cataclysmic History of the Earth* by Noel T. Boaz—**reviewed by John R. Lukacs**

156 *Errata*

Information for Authors

Announcements

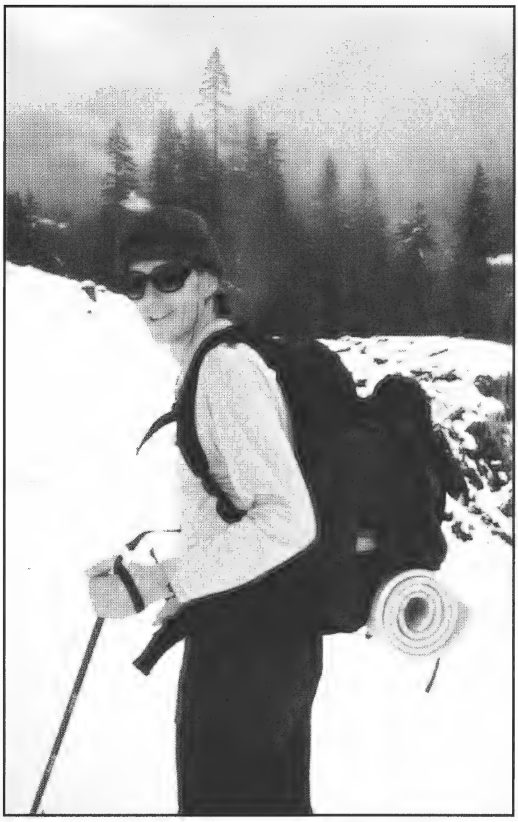
Outstanding Scientist Award



James K. Agee is this year's recipient of the Outstanding Scientist award. He is a Professor of Forestry at the University of Washington, where he has been a faculty member in the College of Forest Resources since 1978. He received his B.S., M.S. and Ph.D. from the University of California, Berkeley. During his tenure at the College of Forest Resources, he served as the Leader of the National Park Service Cooperative Park Studies Unit from 1978 to 1988, and as Professor and Chairman of the Division of Forest Resource Management from 1988 to 1993.

Jim Agee has served on a variety of state, regional, and national committees including stints as a member and Chair of the Washington Natural Heritage Council, and Trustee of the Washington Chapter of The Nature Conservancy. Presently, he serves on the National Academy of Sciences Committee on Sustainability and Future of Non-Federal Forests, the Governor of Oregon Science Team on Eastside Forest Restoration, and the Committee of Scientists tasked with review of the USDA Forest Service planning and National Forest Management Act. He has published widely and is an innovator and leader in the field of fire ecology, publishing *Fire History in Pacific Northwest Forests* in 1993. He is also co-author of the forthcoming book *Forest Health and Protection*.

Jim Agee served as Associate Editor for *Northwest Science* for the past eleven years, stepping down from this position in 1998. He currently serves as Associate Editor for *Ecological Applications*. He is a member of the Ecological Society of America, International Association of Wildland Fire, Natural Areas Association, Northwest Scientific Association, Society for Conservation Biology, and Washington Native Plant Society. Jim Agee has had a distinguished career in science and education, is an exemplary instructor, and has been instrumental in focusing the careers of many fire scientists, foresters, and forest ecologists. His work over the past two decades has contributed extensively in the fields of public policy and regional environmental concerns.



Honorary Life Member Award

David L. Peterson is this year's recipient of the Honorary Life Member award. He received the award upon stepping down as Editor of *Northwest Science*, a position he held for six years. His research and teaching experience in a range of ecological subjects has provided the broad perspective necessary for editorial oversight of a multidisciplinary journal. During his tenure as Editor, the journal changed inside and out, with an increased number of submissions and published articles, new features such as the Forum section, and a new cover design and layout. The Honorary Life Member award was presented in recognition of his contributions to the journal and service to the Association.

A self-described mountain ecologist, Dave Peterson works for the U.S. Geological Survey, Biological Resources Division, and is Professor in the College of Forest Resources, University of Washington. He received his Ph.D. in Forest Ecology from the University of Illinois in 1980, and worked as a research scientist for the Forest Service Pacific Southwest Research Station until he moved to Seattle in 1989. His current research addresses global climate change impacts on forest ecosytems, fire ecology, and air pollution, with a focus on national parks and protected areas in the Pacific Northwest. He has published over 100 scientific papers and has edited three books: *Human Ecology and Climate Change: People and Resources in the Far North; The Role of Restoration in Ecosystem Management;* and *Ecological Scale: Theory and Applications.* He teaches courses on Forest Ecosystem Dynamics and Dendrochronology at the University of Washington, and spends as much time as possible—both personal and professional—in the Cascade and Olympic Mountains.

1998 Student Research Grants

Each year the Northwest Scientific Association awards grants to several students who have submitted outstanding research proposals. Congratulations to this year's research grant winners, who were announced at the 1998 NWSA meeting:

- Stephen Mech, Washington State University, "Effects of habitat fragmentation on small mammal movements"
- Kirsten M. Bohn, Idaho State University, "The impact of a timber harvest on day roost selection by *Lasionycteris noctivagans* and *Myotis evotis* in Cairbou National Forest"
- Brenda McCracken, Eastern Washington University, "Isolation of a fungus and verification of its beneficial mycorrhizal association with *Vaccinium membranaceum* (big huckleberry)"
- Mathew R. Cooper, Eastern Washington University, "Differential success among genotypes of varying defensibility: Can predators drive natural selection in pond populations?"
- Steven A. Trudell, University of Washington, "The effect of mycorrhiza type on nitrogen uptake by plants in an old-growth forested watershed, Olympic National Park, Washington"

New Associate Editors

Northwest Science is pleased to welcome two new Associate Editors.

Dr. Patricia Heglund is Associate Editor for Wildlife Biology. Pat is a research faculty member in the Departments of Biological Sciences and Fisheries and Wildlfe at the University of Idaho, Moscow. She received her Ph.D. from the University of Missouri in 1992 and formerly worked for the U.S. Fish and Wildlife Service in Anchorage. Her research focuses on habitat selection in migratory birds, including neotropical migratory birds in managed landscapes, and she teaches ornithology.

Dr. Michael Feller is Associate Editor for Forestry. Michael is an Associate Professor in the Faculty of Forestry at the University of British Columbia, Vancouver. His research has been conducted throughout British Columbia and focuses on the effects of forest management practices on streams and the ecological effects of prescribed burning, with emphasis on forest nutrient cycling and its natural and management-induced perturbations. He teaches fire science and management and alpine ecology and management, and directs the undergraduate resource conservation program.

Some Parting Words from the Past Editor

The 1990s have been a time of rapidly changing scientific and natural resource issues in the Pacific Northwest. With the paradigm of science-based management becoming more firmly entrenched, state and federal agencies, as well as the general public, are demanding more and better information about our biological and cultural resources. In the background of media hype about forest management, endangered species, and a host of other issues, a few hundred scientists are working diligently to collect the data necessary to address our environmental and social problems. It has been exciting to see so much of their work—both basic and applied science—published in *Northwest Science*. The journal plays a unique role in our region by providing a multidisciplinary forum for scientific issues, rather than being provincially focused on a particular "ology."

I have been privileged to serve as Editor for the journal for six years during a dynamic decade of scientific activity in the Northwest. The quality of published articles has always been my top priority, and I am particularly proud of the fact that we have published so many relevant articles during this period of time. I have worked hard to improve the turnaround time for editorial review and publication, and have encouraged the publication of special issues of the journal on focused topics. From a selfish perspective, this job has allowed me to learn about state-of-the-art science across a wide range of disciplines and to communicate with the remarkably diverse Northwest scientific community. I am grateful to the Northwest Scientific Association for providing me with this opportunity. Linus Pauling once said "the best way to have good ideas is to have lots of ideas." Journals, like the science they represent, are dynamic entities, and the new Editor will be looking for your suggestions to improve the journal. Please send *Northwest Science* your best papers and best ideas!

— David L. Peterson, Past Editor

And a Greeting from the New Editor

I am very much looking forward to being the Editor of *Northwest Science*. I have been a member of the Northwest Scientific Association for nearly 25 years and have long appreciated our journal—I now have the opportunity "give something back." It is my intent to maintain the high standards set by my predecessors and to continue publishing high quality articles in *Northwest Science*. To this end, I *strongly encourage* my fellow members in the Association to submit articles for potential publication in the journal. I also sincerely thank the Board of Trustees for this opportunity, and David L. Peterson and Nancy Grunewald for the improvements they have made in *Northwest Science*. I will do my best to continue in this tradition.

— Edward G. Schreiner, Editor

Minutes of the 1998 Northwest Scientific Association Board of Trustees Meeting (25 March) and Business Meeting (27 March), Olympia, Washington

Board of Trustees Meeting

The meeting was called to order by President Cellarius at 4:15 PM.

Members Present: David Hansen, Ted Thomas, Nancy Grunewald, Richard Cellarius, Barry Keller, David Peterson, Ed Schreiner, Gabe Tucker (Program Chair), Paul McDaniel, Roger Rosentreter, Kurt Othberg, Peggy O'Connell.

Members Absent: R. Carr, K.A. Miller, M. Sheehan, J. Koprowski, R. Matthews, M. Pitt, H. Brown, M. Hemstrom.

Minutes of the 26 March 1997 Board Meeting and 4 October 1997 Board Meeting were read and approved

Peggy O'Connell reported that she had received a box of NWSA papers from Denis Lavender and had organized these. The papers include minutes and correspondence from 1979 to the present. N. Grunewald announced that archival information (abstracts from meetings, copies of minutes, official documents) from the beginning of the society is housed in the Archival section of the WSU Library. Lawrence Stark is the contact (509-335-8679). P. O'Connell distributed a list of Outstanding Scientist Award recipients from 1960 to present (award had been started in 1960).

The Treasurer's report was read by Dave Hansen. Total assets at end of 1997 were $41,306.36 and at 15 March 1998 were $50,072.35. Although the 1997 Income/Expense statement indicates a deficit (-$6,194.54), this reflects the timing of receipt and deposit of membership dues rather that a shortfall. The 1998 Income/Expense statement-to-date indicates a positive balance ($8,765.99). The major expenses, as always, are the WSU Press bill (which will increase from ca. $7,000 to ca. $9,000 this year) and student awards. Credit card charges have increased due to more members charging their dues. Membership increased in 1997 (452) relative to previous years (1996-409; 1995-429; 1994-428; 1993-424). Total membership is 352 for 1998, but this should go up.

There was continued discussion of finances and membership. D. Hansen indicated, in response to a question from R. Black that the $45-50,000 total assets had held steady during the last decade. R. Cellarius asked whether the increase in dues had impacted membership. D. Hansen replied that it increased income, but didn't affect membership. R. Cellarius asked if D. Hansen had membership brochures for registration table at meeting. D. Hansen said that he was all out. R. Cellarius will get something out by tomorrow for the table.

Dave Peterson gave the Editor's Report. The submission rate has increased during the last 2-3 years; submissions have been at record pace since January, with many papers in Wildlife area. There has been a steady rate of acceptance at 50%. Two good associate editors stepped down: Jim Agee and Gerry Wright. The new associate editors are Patricia Heglund (University of Idaho) in Wildlife Biology and Michael Feller (University of British Columbia) in Forestry. Three special issues are in the works: Large-scale fire effects (1998), Forestry Practices in British Columbia (late 1998), and Ecosystem management options in the PNW (1999). There have been other requests, but we are limited to one per year. Turnaround time has improved: 6 months from submission to acceptance and 9-10 months from submission to publication.

Editorial Committee: Tim Reynolds indicated that at October meeting R. Cellarius felt there should be a policy about notes. An Editorial Board was formed with T. Reynolds (chair), D. Peterson, and N. Grunewald , and two volunteers from general membership. The response from the general membership was great and the two members are Mary Barkworth (Utah State University) and Winston Smith (USFS–Juneau). The two immediate goals of the committee were to: 1) assist in recruiting a new Editor, 2) develop a policy about notes. T. Reynolds distributed a position statement suggesting that NWSA

should accept notes if they have adequate scientific merit. The statement was expanded to include review/bibliographic articles. The recommendation of the Editorial Board was accepted and approved.

Ed Schreiner was introduced to the Board and was nominated and approved as new Editor of *Northwest Science*.

Meetings: R. Cellarius reported that there were 280 preregistrants and now >300 paid registrants, 150 abstracts (a few have withdrawn). He has worked closely with the Society for Northwest Vertebrate Zoology (Larry Jones). Gabe Tucker indicated that he didn't get a big response from social, geology, and laboratory sciences and the emphasis is on natural and applied sciences.

R. Black reported on the 1997 Meeting. He expressed his thanks to G. Tucker. The 1997 meetings ended up with a $9.97 earning, but we did get a check from the EWU Provost for $2000 which would be split with provost after the meetings. Therefore $1,009.97 will be sent to D. Hansen.

1999 Meetings: R. Black reported that Bob Carr has put a lot of effort into locating a 1999 meeting site, with no firm commitment to date. Possibilities include Western Oregon State College, Portland State University, and a joint meeting with the March 1999 Mt. Rainier centennial science meeting at U. Washington-Tacoma. Board members favored coordinating with the Mt. Rainier meeting, and the Program Committee (B. Carr, B. Keller, and D. Hansen) will address this in the near future.

Nominating Committee: P. O'Connell reported that Ted Thomas has agreed to serve as President for NWSA 1998-2000 and that the nominating committee was pleased to put his name forward to the board. The nomination was approved.

P. O'Connell reported that the 15 board members should be equally distributed between the 3 years of rotation, and that this year we are off -balance and need to have 3 more trustees whose terms go until 1999; 5 for the next 3-year term; and 1 trustee to complete the term of T. Thomas.

The Nominating Committee nominated Ross Black, Barry Keller, and Roger Rosentreter for 1-year extension terms, and the following people trustees candidates were nominated and approved for consideration by the general membership: R. Rosentreter (1999), B. Keller (1999), R. Black (1999), C. Halpern (2000), S. Sillet (2001), S. Hacker (2001), D. Zabowski (2001), K. Kardong (2001), L. Broberg (2001).

Honors and Awards: R. Rosentreter reported that Jim Agee (University of Washington) is the 1998 recipient of the Outstanding Scientist award. Dave Peterson is the recipient of the Honorary Life Membership for his service to the society.

Student Awards: There were 9 proposals and recommendations for 5 awards. The awards were to be announced at the banquet and published in the next issue of *Northwest Science*.

Long-range Planning: R. Cellarius asked R. Black whether he had information about long-range planning from Bob Carr. R. Black indicated that B. Carr wants to encourage the president to lead a quest for where we are going and how we are going to get there. R. Cellarius stated that he thought divorcing the presidency from the meetings was a good idea. D. Peterson suggested that we need to work on development (membership and institutional membership).

Tax Status: B. Keller announced that NWSA is now back on 501-C(3) status. The next question is about our current status with the state of Washington. We need to submit information about the board to the state on a yearly basis and we need a permanent registered agent. We need to find out state regulations. If we do need to reincorporate, B. Keller suggested that we do so in another state, perhaps Idaho where, for a $25 dues, NWSA could join an organization to reinvest money with 15-18% return and the organization would do all paper work associated with gifts to NWSA. We need to print that we are 501-C(3) status in the journal and need to print request for gifts (that would go toward, e.g., student awards, meetings).

Business Meeting

The meeting was called to order by President Richard Cellarius. There were 45 members and officers present.

The minutes of the 26 March 1997 Business Meeting were distributed and read by Peggy O'Connell. The minutes were approved.

The Treasurer's report was distributed and approved.

Tim Reynolds, chair of the Editorial Committee, gave the *Northwest Science* report. He reviewed that the function of the Editorial Committee was to develop editorial policy concerning notes and to recruit a new editor and associate editors. T. Reynolds summarized the Editor's Report that Dave Peterson had presented to the Board. T. Reynolds announced that Dave Peterson has stepped down as Editor and that Ed Schreiner will be the new Editor.

Roger Rosentreter, chair of the Awards Committee, announced that Jim Agee is the recipient of the NWSA Outstanding Scientist for 1998 and Dave Peterson received an Honorary Life Membership. R. Rosentreter then requested that members of NWSA send names of nominees for the two awards to him.

Jerry Wolff, chair of the Student Awards Committee announced the 5 recipients of the 1998 Student Research Awards: Steve Mech (WSU), Kirsten Bohn (ISU), Matt Cooper (EWU), Brenda McCracken (EWU), and Steve Trudell (UW). He encouraged students to apply for these awards.

Ross Black, Program Chair for the 1997 meetings, reported that there had been 219 registrants and 118 papers presented at last year's meeting. There would be $1,009.25 earnings returned to NWSA.

Richard Cellarius reported that there have been 350 registrants and 150 Abstracts at this year's meeting. He acknowledged the cooperation of the Society for Northwest Vertebrate Zoology in organized the joint meeting. R. Cellarius announced that, to date, there is no firm site for the 1999 meetings but that Bob Carr has been working on this. R. Cellarius announced that there is a possibility of having a joint meeting in conjunction with the centennial celebration of Mt. Rainier, possibly at University of Washington at Tacoma.

Peggy O'Connell presented the Nominating Committee's nominations for officers and trustees. The committee put forward the nomination of Ted Thomas as President of NWSA (1998-2000). Richard Cellarius asked for further nominations from the floor. Hearing none, the membership elected T. Thomas as President.

P. O'Connell reported that the 15 NWSA trustees should be equally distributed between the 3 years of rotation. The nominees (see minutes of the Board meeting above) were presented to the NWSA membership. R. Cellarius asked for further nominations. Hearing none, the membership elected all of the nominated candidates.

Richard Cellarius expressed his thanks to the board and the membership for their support during his term as President.

Ted Thomas expressed the thanks of the board and the membership to Richard Cellarius for serving as the NWSA President. He said he was pleased and excited to be the new President of NWSA and looked forward to building the journal and the association.

The meeting was adjourned at 1:00 PM.

Jaroslav Dobrý[1,2], and **Karel Klinka**[1],
[1]Forest Sciences Department, University of British Columbia, Vancouver, British Columbia, Canada, V6T 1Z4
[2]Institute of Botany, Czech Academy of Sciences, 252 43 Pruhonice, Czech Republic

Reconstructing Temperature from Tree Rings of Pacific Silver Fir in Coastal British Columbia

Abstract

We used ring-width (RW) and maximum latewood density (MLD) chronologies for high-elevation Pacific silver fir (*Abies amabilis* Dougl. *ex* Forbes) from the Coastal Western Hemlock zone near Vancouver, British Columbia to reconstruct April to September mean temperatures for the 1770 -1990 period. The reconstruction was based on a calibration and verification procedure. The best reconstruction result was achieved when both RW and MLD chronologies were utilized. The reconstruction agreed with that produced for interior British Columbia from densitometric data. We suggest that rings of Pacific silver fir, growing under the influence of a perhumid maritime cool mesothermal and subalpine boreal climates in the Pacific Northwest, can serve as proxy-climate indicators.

Introduction

In regions with discrete growing seasons, annual growth rings of trees can serve as unique proxy-climate indicators providing year-to-year climatic variations are great enough to affect growth and be reflected in the characteristics of rings (Fritts 1970; Briffa et al. 1988). Tree ring analysis of high-elevation species, in particular, can yield information on past temperature fluctuations because at high-elevations growing season temperature can be the factor most limiting cambial activity and ring formation (Fritts 1970, Graumlich and Brubaker 1986, Luckman 1997).

The methodology of climate reconstruction from tree-ring data and the problems encountered were discussed by Fritts (1976, 1991), Lofgren and Hunt (1982), Gordon (1982), Pittock (1982), and Meko et al. (1980). In the Pacific Northwest, several temperature reconstruction were made with varying degree of success. For example, Graumlich and Brubaker (1986) reconstructed annual temperature from tree rings trees at timberline in the Cascade Range of Washington; however, Briffa et al. (1992) was only partly successful when reconstructing summer temperature patterns for northern Alaska and northwestern Canada because of uncertainties in the extreme northern portion of their grid.

Most of the tree ring studies in the Pacific Northwest, however, were conducted outside the coastal region in more continental climates. The data that do not capture unique features of rings of the trees that have grown under the influence of maritime climate may result in faulty climatic reconstruction for the coastal region (Fritts 1991). This study represents the first attempt in the coastal region of British Columbia to reconstruct growing-season temperature using ring-width and maximum latewood density chronologies of Pacific silver fir.

Although the conifers of this maritime region show complacent growth patterns with weak climatic signals, common signals (marker rings) have been found in several tree species, such as Pacific silver fir and western redcedar [*Thuja plicata* (Donn *ex* D. Don) Lamb.] (Dobrý et al. 1996). Of the species investigated, the ring-width and maximum-latewood-density chronologies for Pacific silver fir from montane and subalpine sites in the North Shore Mountains (near Vancouver, B.C.) had the strongest climate signals as determined by response functions. This finding suggests that these chronologies might have potential as proxy-climate data. Thus the objectives of the present study were (1) to determine the utility of Pacific silver tree-rings for a local climatic reconstruction and (2) to make comparison with other temperature reconstructions done for the Pacific Northwest (e.g., Graumlich and Brubaker 1986, Schweingruber et al. (1991).

Materials and Methods

As proxy-climate data, we used ring widths (RW) and maximum latewood densities (MLD) chronologies that were developed for Pacific silver fir from trees growing on a high-elevation site in

© 1998 by the Northwest Scientific Association. All rights reserved.

the transition between the Coastal Western and Mountain Hemlock biogeoclimatic zones (Klinka et al. 1991) within the Greater Vancouver Watershed District (Dobrý 1994, Dobrý et al. 1996). Both zones are influenced by a very wet, maritime climate; the Coastal Western Hemlock zone by a cool mesothermal climate, and the Mountain Hemlock zone by a subalpine boreal climate (Klinka et al. 1991). The study site was situated in Eastcap Creek, Capilano Watershed (1000 m asl, 49° 31' N, 123° 04' W).

RW and MLD measurement series were crossdated by the COFECHA program and only the best inter-correlated series were selected for developing chronologies using the ARSTAN standardization program (Grissino-Mayer et al. 1994). Standard chronologies were developed using default detrending option (negative exponential curve or linear regression and cubic smoothing spline). RW and MLD indices were computed by division and subtraction, respectively.

Residual chronologies were modeled by autoregression to remove most of the low-frequency trend and to emphasize the common high-frequency variation in the chronologies. The RW chronology (coded CA1; 16 trees, 32 cores) spanned the period of 307 years, and the MLD chronology (coded CA2; 7 trees, 7 cores) 238 years. However, for reconstruction we utilized only the 1769–1990 and 1770–1991 period in the RW and MLD chronologies, respectively, so that density series from at least 5 trees could be included into the MLD chronology in any particular year of the period used for reconstruction.

The climatic data for reconstruction came from the Agassiz station, located approximately 100 km east of Vancouver (49° 15' N, 121° 46' W, 15 m asl.). This station provided the longest continuous climatic data for the study area. A few missing records in the data were computed by linear regressions using the data from the neighboring Chilliwack station.

Simple correlations and response functions for RW and MLD chronologies were computed by the PRECON program (Fritts 1994) to determine which of the 34 available climatic parameters (monthly temperature and precipitation from the previous May through September of the current year) were to be selected and tested in transfer functions. The results of simple correlations and response functions were integrated in one figure (see Figure 1). For temperature reconstruction we selected that chronology from among standard and residual RW and MLD chronologies that had the strongest correlation with climatic data. Linear regression was used to quantify climate – growth relationships.

We used transfer functions (Fritts 1976) to describe the relationship between climate and tree-ring data. To select the most suitable climatic parameter for a transfer function, we matched both chronologies and corresponding climatic data for a calibration period following the methodology described in Fritts (1976), Lofgren and Hunt (1982), and Conkey (1986). A two-step process was applied for developing transfer functions. In the first step we developed transfer functions for each RW and MLD chronology. When using the RW chronology, we examined relations of ring-width indices in the current year to the mean monthly temperature in (a) July, (b) July and August, and (c) June through August of the previous year. When using the MLD chronology, we examined current year temperature data for each individual month from March through September, and for the period of April through September as it was done by Schweingruber et al. (1991). In the second step, we developed the transfer functions based on both the RW and the MLD chronologies.

In developing transfer functions, we followed the 2-step calibration-verification scheme applied by Briffa et al. (1988, 1992). In the first step, for the first calibration period of 1892–1941 (early calibration), the late period from 1942 to 1990 was used for verification, and inversely, for the second calibration period of 1942–1990 (late calibration), the early period of 1982 to 1941 was used for verification. In the second step, we examined the stability of the developed linear regression model using the procedure of Graumlich (1985) and used five additional randomly selected data sets, each with 50 years for the first part and 49 years for the second part.

We used several tests to verify the reliability of reconstruction (Gordon and LeDuc 1981; Fritts et al. 1990; Fritts 1991). The tests were computed using the 'verify' routine (VFY) of the Dendrochronology Program Library (DPL) software (Holmes 1994). From all the tests done, we selected only those used by Grissino-Mayer (1996)

for presentation: (1) correlation coefficient, (2) reduction of error (RE), (3) products-means test, and (4) sign-products test.

Correlation coefficient reflects the entire spectrum of variation that is common between two data sets. RE statistics provides a sensitive measure of reliability because it estimates fairly accurately the explained variance. The products-means test calculates the products of the deviations and collects the positive and negative products in two separate groups based on their signs. The values of the products in each group are summed, the means are computed, and the difference between the absolute values of the two means is tested for significance. The sign-products test is a less sensitive measure of reliability; it enumerates the frequency of agreements and disagreements of the signs of departures from the sample means. If the test is successful, it can be concluded that the sign of the estimate is more often correct than would be expected from random numbers.

We tested for the normality of differences between actual and reconstructed temperatures using the Kolmogorov-Smirnov goodness of fit (Zar 1984). Following the verification of the transfer functions developed following the calibration-verification procedure (i.e., the early and late calibration-verification), we used the entire 1892–1990 period of climatic and tree-ring data to develop a new transfer function for temperature reconstruction.

Temporal patterns of actual and reconstructed temperatures in the 20th century were examined by polynomial regression (Luckman 1997). Comparison between our reconstructed temperatures and those reported by Schweingruber et al. (1991) was done using a sign-products test (with normal approximation) that compared the agreement between the positive and negative departures of the reconstructed values from the mean values.

Results

Response functions for the residual RW- and the standard MLD chronologies showed which climatic parameters were suitable for developing transfer functions. In both correlations and response functions, there was a significant response of RW to July temperature of the previous year and a significant response of MLD to March, April, May, and August temperature of the current year. The response profiles for precipitation showed (i) significant positive responses of RW to August precipitation of the previous year and to May precipitation of the current year, (ii) a negative response to July precipitation of the current year, and (iii) significant negative responses of MLD to November precipitation of the previous year and to September precipitation of the current year (Figure 1).

The correlation coefficients between mean July–August temperature of the previous year and the RW chronology index in the current year were $r = -0.33$ and $r = -0.44$ for the standard and residual chronologies, respectively. The transfer function model based on residual chronology ($T_{t-1} = 19.597 - 1.712(RW_t)$; $n = 99$; $R^2 = 0.19$; $p < 0.001$) passed 83% of the verification tests using the following criteria: correlation coefficient, reduction of error, T-value of products-means test, and sign-products test (including additional five randomly selected data sets, i.e., twelve tests for one criterion).

We used the standard MLD chronology for temperature reconstruction because it was better correlated with the mean growing-season temperature in the current year than residual MLD chronology (mean sensitivity = 0.06, and the first order autocorrelation = 0.15). Following Schweingruber et al. (1991), we examined the current year temperature data for each individual month from March through September, and for the period of April through September. Since the April through September period gave the strongest correlation ($r = 0.57$), it was used in the MLD transfer function model ($T_t = 8.316 + 6.561(MLD_t)$; $n = 99$; $R^2 = 0.32$; $p < 0.001$). Similar to the RW model, the MLD model passed all verification tests except for one of the twelve sign-products tests. The calibration and verification statistics indicated a considerably stronger climate-growth relationship for the MLD than RW chronology.

In the second step, we developed the transfer functions based on both the RW and the MLD chronologies. Correlation between these chronologies was not significant ($r = -0.21$; $p = 0.40$), indicating independence of predictor variables. In consequence, we used multiple linear regression to analyze climate - growth relationship and both chronologies to estimate the mean April – September temperature. Verification tests showed an improvement in the performance of the climate – growth model as a result of combining the chro-

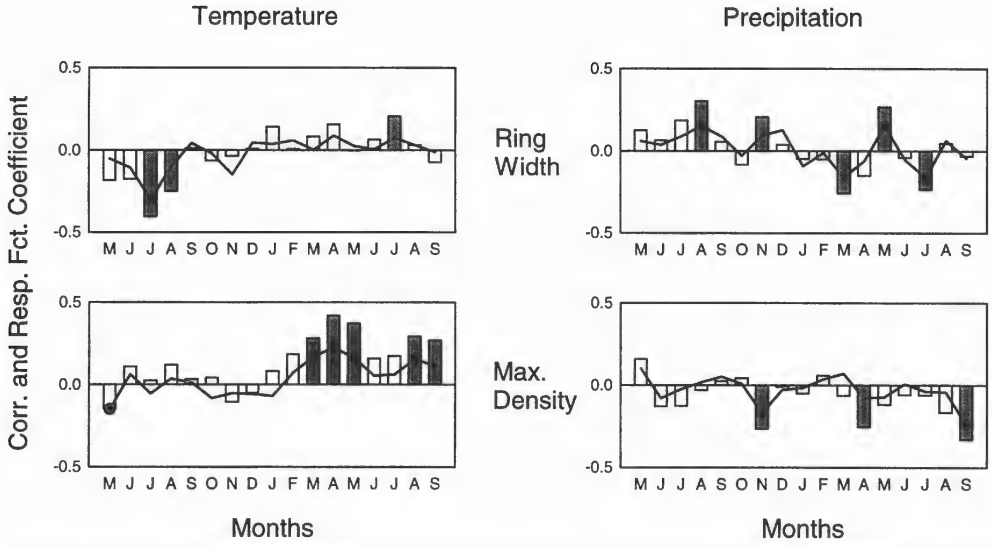


Figure 1. Correlations (bars) and response functions (lines) for indices of ring width and maximum late wood density *Abies amabilis* chronologies on mean monthly precipitation and temperature (May of the previous year to September of the current year) for the period of 99 years. Months with significant positive or negative relations between climate and RW or MLD indices are indicated by filled bars or circles, respectively .

TABLE 1. Calibration and verification statistics for the April–September mean temperature reconstruction based on the ring-width and standard maximum latewood chronologies. Part A: 1—verification (1942-1990) for the early calibration (1892-1941), and 2 through 6—verification for five randomly selected data sets of 49/50 years; part B: 1—verification (1892-1941) for the late calibration (1942-1990), and 2 through 6—verification for five randomly selected data sets of 50/49 years. Values significant at the 95% confidence level are marked with an asterisk. Any positive RE value can be considered significant.

Criterion	Part	Data set						Mean
		1	2	3	4	5	6	
Correlation coefficient								
	A	.60 *	.66 *	.67 *	.58 *	.55 *	.51 *	.60
	B	.64 *	.59 *	.55 *	.66 *	.66*	.69 *	.63
Reduction of error (RE)								
	A	.30	.38	.45	.36	.22	.23	.32
	B	.38	.28	.30	.46	.38	.45	.38
T-value of Products-means test								
	A	3.23 *	3.47 *	3.42 *	3.70 *	3.12 *	2.73 *	3.28
	B	3.40 *	3.65 *	3.73 *	3.56 *	3.77 *	4.68 *	3.80
Sign-products test								
	A	13 *	11 *	14 *	13 *	19	16 *	14
	B	17 *	18 *	21	16 *	13 *	17 *	17

nologies (Table 1). Normality of differences between actual and estimated values was significant at the 95% confidence level. The final transfer function was recalibrated as follows:

[1] $T_{t-1} = 9.697 + 5.922(MLD_{t-1}) - 0.742(RW_t)$
Adjusted $R^2 = 0.37$ $p < 0.001$ $n = 99$

where T_{t-1} is the predicted mean April–September temperature of the previous year, MLD_{t-1} is the maximum latewood density in the previous year, and RW_t is the ring-width index in the current year.

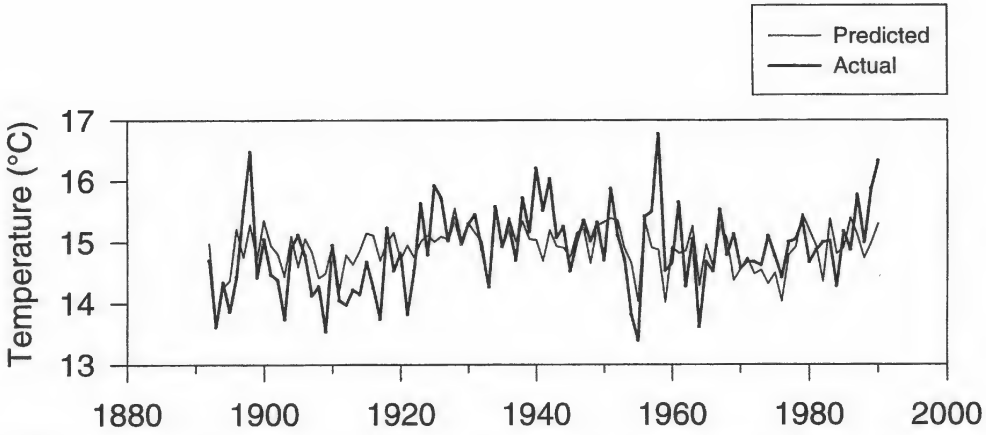


Figure 2. Comparison between actual April - September mean temperatures and the values predicted by the RW and MLD chronologies over the 1892-1990 period.

The actual and predicted April–September mean temperatures for the 1892-1990 period are plotted in Figure 2. Correlation between the actual and predicted temperatures was moderately strong ($r = 0.57$). 'Extreme' years were more poorly predicted than 'moderate' years. For high-pass filtered actual and predicted temperatures, the short-term variation of these two time series was well correlated ($r = 0.68$). The low-frequency component of the reconstructed temperatures for the 1770–1990 period had the same mean and the same low-frequency variation as the original data, and showed alternating periods with predominantly higher or lower reconstructed temperatures, respectively (Figure 3). The sign-products test (148 agreements, 62 disagreements, $p < 0.001$) showed agreement between reconstructed temperatures in this study and Schweingruber et al. (1991).

Discussion

The significant negative correlation between July - August temperature of the previous year with RW of the current year was consistent with the results of Ettl and Peterson (1995) and Garfinkel and Brubaker (1980) who also suggested a significant negative correlation of ring-width with July temperature of the previous year. A possible explanation for the significance of the previous late summer temperature is that it reduces foliage loss during a late summer moisture stress and allocate stored assimilates for the use in the next growing thus positively affecting ring width in the next growing season (cf. Larsen and MacDonald, 1995).

Better correlation of standard than residual MLD chronologies with the temperature data

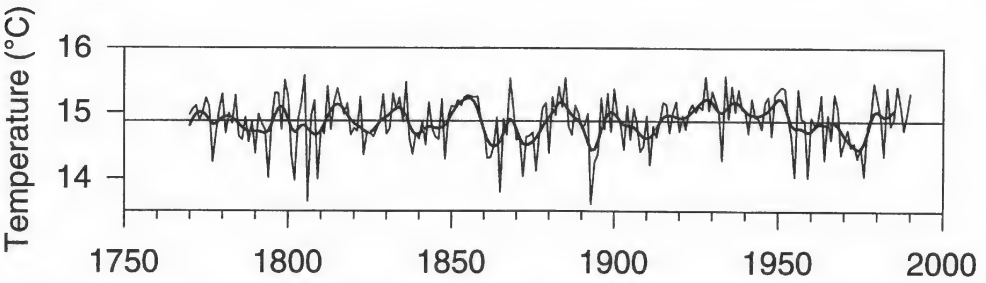


Figure 3. Reconstruction of April - September mean temperatures over the 1770-1990 period for Vancouver, British Columbia. The smoothed line is for the same data passed through a 13-yr low-pass filter.

appears to reflect some lower frequency temperature variations as suggested by D'Arrigo et al. (1992). The verification of transfer functions indicated that the model based on the MLD chronology was superior than that based on the RW chronology. Using both RW and MLD chronologies as combined proxy-climate data resulted in a further improvement of the model. The stability of the model was confirmed by verification tests that gave very similar results when using different data sets.

A year-by-year comparison of reconstructed temperatures in this study agreed with the temperature isolines maps for western North America by Schweingruber et al. (1991), despite the fact that they used tree-ring density data from more continental inland sites of British Columbia. There was no significant relationship between our reconstruction and that of Fritts (1991, and personal communication) who also used ring-width chronologies from inland sites, such as from the Kamloops region.

Some of the differences between these reconstructions might be a result of the differences in the strength of temperature signals between maximum latewood densities and ring-widths or the differences in climatic patterns between more maritime and continental sites. The reconstructed April through September mean temperature in this study had some very similar features to the reconstructed mean annual temperature for Longmire, Washington (Graumlich and Brubaker 1986). In both reconstructions, there was a greater variation of reconstructed temperatures in the first decade of the 19th century. The cool episodes in 1860s, 1870s and 1890s in our reconstruction for the coastal region correspond with the cool episodes from 1860 to 1890 for Longmire. Furthermore, the rise of temperature in the first half of the 20th century detected in this study corresponds to that reported for Longmire.

When comparing temporal patterns between actual and reconstructed temperatures in this study for the 20th century by polynomial regression, the fitted lines of the third order regression ($p < 0.001$) had the same shape. This indicates a general conformity between tree-ring characteristics and a warming trend in the 20th century. The curves were similar to polynomial regressions used by Luckman (1997) to characterize long-term trends in the records of mean annual temperature of one station in the Canadian Rocky Mountains. He differentiated two general patterns in the polynomial curve shape and suggested that they may reflect some influence of maritime and continental climates on the climate of the area. The shape of our fitted polynomial lines had the position in between these two patterns.

Our reconstruction also agreed with that developed for the Pacific Northwest by Briffa et al. (1992). All of their negative (1810, 1876, 1880, 1899) and positive (1772, 1776 1796, 1915) extreme years corresponded in the direction of their departure from the mean value with our data. The long-term variation in our reconstructed temperatures in both studies showed several periods with similar positive or negative departures in the smoothed data from the mean values: warmer periods in 1790s, 1850s, and during 1920-1950, and a cool episode in 1890s. The longest warm period in our reconstruction, which is outside the climatic record, occurred from 1848 to 1858 AD (Figure 3).

We concluded that the tree-rings of Pacific silver fir growing in the montane and subalpine coastal forests of British Columbia under a strong influence of a perhumid maritime cool mesothermal or subalpine boreal climate have a promising potential as local proxy-climate indicators.

Acknowledgements

The authors are indebted to Josef. Kyncl, Institute of Botany, Czech Academy of Sciences, who kindly contributed densitometrical data. We wish to thank Harold C. Fritts, Laboratory of Tree-Ring Research, University of Arizona, and Malcolm K. Cleveland, Tree-Ring Laboratory, Department of Geography, University of Arkansas, for valuable comments on an early draft of the manuscript. The financial support provided by the Natural Science and Engineering Council of Canada and Forest Renewal British Columbia is gratefully acknowledged.

Literature Cited

Briffa, K. R., P. D. Jones, and F. H. Schweingruber. 1988. Summer temperature patterns over Europe: A reconstruction from 1750 A.D. based on maximum latewood density indices of conifers. Quaternary Res. 30: 36-52.

Briffa, K. R., P. D. Jones, and F. H. Schweingruber. 1992. Tree-ring density reconstructions of summer temperature patterns across western North America since 1600. J. Climate 5: 735-754.

Conkey, L. E. 1986. Red spruce tree-ring widths and densities in eastern North America as indicators of past climate. Quaternary. Res. 26: 32-243.

D'Arrigo, R. D., G. C. Jacoby, and R. M. Free. 1992. Tree-ring width and maximum latewood density at the North American tree line: parameters of climatic change. Can. J. For. Res. 22: 290-1296.

Dobrý, J. 1994. Tree-Ring Data, Pacific shore. International Tree-Ring Data Bank. IGBP PAGES/World Data Center, Paleoclimatology Data Contribution Series # 94-010. NOAA Paleoclimatology Program, Boulder, Colorado.

Dobrý, J., J. Kyncl,. K. Klinka, and B. A .Blackwell. 1996. Climate signals in coastal old-growth forest trees near Vancouver, British Columbia. *In* J. S. Dean, D. M. Meko, and T. W. Swetnam (eds.) Tree Rings, Environment and Humanity. Radiocarbon. Pp. 733-741.

Ettl, G. J. and D. L. Peterson. 1995. Growth response of subalpine fir (*Abies lasiocarpa*) to climate in the Olympic Mountains. Global Change in Biology 1: 213-230.

Fritts, H. C. 1970. Tree-ring analysis and reconstruction of past environments. Vancouver, University of British Columbia Faculty of Forestry, Bull. No. 7: 92-98.

Fritts, H. C. 1976. Tree Rings and Climate. New York, Academic Press.

Fritts, H. C. 1991. Reconstructing large-scale climatic patterns from tree-ring data. A diagnostic analysis. The University of Arizona Press, Tucson/London.

Fritts, H. C. 1994. PRECON 4.0 Upgrade (Diskette). Dendrochronological Modeling, Harold C.Fritts, 5703 North Lady Lane, Tucson, Arizona 85704-3905.

Fritts, H.C., J. Guiot, G.A. Gordon, and F.H. Schweingruber. 1990. Methods of calibration, verification and reconstruction. *In* E. Cook and L. Kairiukstis (eds.) Methods of Dendrochronology. Applications in the environmental sciences. Dordrecht, The Netherlands, Kluwer Academic Publishers. Pp. 163-217.

Garfinkel, H. L., and L. B. Brubaker. 1980. Modern climate–tree-growth relationships and climatic reconstruction in sub-Arctic Alaska. Nature 286:72-874.

Gordon, G. A. 1982. Verification of dendroclimatic reconstructions. *In* M. K. Hughes, P. M. Kelly, J. R. Pilcher, V. C. LaMarche, Jr., and al. (eds.) Climate from Tree Rings. Cambridge University Press, Cambridge. Pp 58-62.

Gordon, G. A, and S. K. LeDuc. 1981. Verification statistics for regression models. *In* Preprints, Seventh Conference on Probability and Statistics in Atmospheric Sciences, Session 8, November 2-6, 1981, Monterey, California. American Meteorological Society, Boston. Pp. 129-133.

Graumlich, L. J. 1985. Long-term records of temperature and precipitation in the Pacific Northwest derived from tree rings. College of Forest Resources, University of Washington, Seattle. Ph.D. Dissertation.

Graumlich, L. J. and L. B. Brubaker. 1986. Reconstruction of annual temperature (1590-1979) for Longmire, Washington, Derived from tree rings. Quaternary Res. 25: 223-234.

Grissino-Mayer, H. 1996. A 2129-year reconstruction of precipitation for northwestern NewMexico, USA. *In* J. S. Dean, D. M. Meko, and T. W. Swetnam (eds.) Tree Rings, Environment and Humanity. Radiocarbon. Pp. 191-204.

Grissino-Mayer, H., R. Holmes, and H. C. Fritts. 1994. International Tree-Ring Data Bank Program Library, Version 1.1 (Diskette). Laboratory of Tree-Ring Research, University of Arizona, Tucson, Arizona.

Holmes, R. L. 1994. Dendrochronology Program Library (Diskette). Laboratory of Tree-Ring Research, University of Arizona, Tucson, Arizona.

Klinka, K., J. Pojar, and D. V. Meidinger. 1991. Revision of biogeoclimatic units of Coastal British Columbia. Northwest Science 65: 32-47.

Larsen, C.P.S., and G.M. MacDonald. 1995. Relations between tree-ring widths, climate, and annual area burned in the boreal forest of Alberta. Can. J. For. Res. 25: 1746-1755.

Lofgren, G. R., and J. H. Hunt. 1982. Transfer functions. *In* M. K. Hughes, P. M. Kelly, J. R. Pilcher, V. C. LaMarche, Jr., et al. (eds.) Climate from Tree Rings. Cambridge, Cambridge University Press. Pp. 50-58.

Luckman, B.H. 1997. Developing a proxy climate record for the last 300 years in the Canadian Rockies - some problems and opportunities. Climatic Change 36: 455-476.

Meko, D.M., C.W. Stockton, and W.R. Boggess. 1980. A tree-ring reconstruction of drought in Southern California. Water Resources Bull. 16: 594-600.

Pittock, A. B. 1982. Climatic reconstructions from tree rings. *In* M. K. Hughes, P. M. Kelly, J. R. Pilcher, V. C. LaMarche, Jr., et al. (eds.) Climate from Tree Rings. Cambridge University Press, Cambridge. Pp. 62-67.

Schweingruber, F. H., K. R. Briffa, and P. D. Jones. 1991. Yearly maps of summer temperatures in western Europe from A.D. 1750 to 1975 and western North America from 1600 to 1982: Results of a radiodensitometrical study on tree rings. Vegetatio 92: 5-71.

Zar, J.H. 1984. Biostatistical Analysis. Prentice-Hall, Inc., Englewood Cliffs, N.J.

Received 30 July 1997
Accepted for publication 30 January 1998

A.R. Tiedemann and **R.R. Mason,** Pacific Northwest Research Station, 1401 Gekeler Lane, LaGrande, Oregon 97850

B.E. Wickman, Pacific Northwest Research Station, Bend, Oregon 97701.

Forest Floor and Soil Nutrients Five Years after Urea Fertilization in a Grand Fir Forest

Abstract

Five years after thinning and fertilization with 350 kg ha^{-1} of N as urea in an interior Pacific Northwest grand fir (*Abies grandis* (Dougl.) Forbes) forest, we measured concentrations of total carbon (C), nitrogen (N), phosphorus (P), sulfur (S), and potassium (K) in the forest floor and upper 30 cm of soil. Effect of fertilization and thinning treatments on available N, P, S, and K in the soil was determined by bioassay with barley as a test plant in a growth chamber experiment. Field treatment combinations were: control; not thinned, fertilized (NT-F); thinned, not fertilized (T-NF); and thinned, fertilized (T-F). Total N concentration of the forest floor was substantially and significantly greater for the NT-F treatment than the other three treatments. This finding supported results of other studies that the forest floor retained a substantial portion of applied N. We did not detect any differences among thinned and fertilized treatments and the control for concentrations of soil total C, N, P, K, or S. Also, availabilities of N, P, and K in soil from thinned and fertilized treatments were the same as the control. Thus, there was no detectable effect of N fertilization on total or available N after 5 years. The salient feature of the bioassay trial was reduced availability of soil S with the NT-F treatment compared to the control and the T-NF treatment. Availability of S was also lower for the TF treatment compared to T-NF treatment. Application of a large quantity of N at this site with extant low levels of soil S further depressed S availability. Nitrogen fertilization should be supplemented with S in sites where soil S levels are comparable to those we observed (0.008%).

Introduction

Forest fertilization has become an attractive option for forest managers to offset nutrient limitations in soils of forested sites and to maintain or enhance growth of coniferous species (Moore 1988, Chappell et al. 1992, Miller et al. 1992). Periodic annual increment in unthinned Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) stands of western Oregon and Washington responded to nitrogen (N) fertilization with a 2.9 to 6.0 m^3 ha^{-1} yr^{-1} increase in growth at 224 kg ha^{-1} of N and 3.8 to 6.2 m^3 ha^{-1} yr^{-1} increase at 448 kg ha^{-1} of N (Peterson and Hazard 1990). Enhancement of growth and yield is the most common reason to fertilize forests, but fertilization also shows promise as a means of ameliorating the effects of insects such as the western spruce budworm (*Choristoneura occidentalis* Freeman) on tree vigor and growth (Mason et al. 1992). Wickman et al. (1992) found that fertilization with 350 kg ha^{-1} N as urea significantly reduced defoliation, increased biomass of shoots, and increased radial growth and height growth of grand fir (*Abies grandis* (Dougl.) Forbes). Height growth of fertilized trees was almost double that for unfertilized. The integrated response was an improvement of 140% in growth efficiency as measured by wood production per unit of leaf area on thinned and fertilized plots (Waring et al. 1992). By the fifth year after treatment, radial growth of grand fir with fertilized treatments was still significantly greater than the control (Wickman et al. 1992), suggesting protracted enhancement of N availability.

Even though the importance of a balanced supply of nutrients for plant growth is well understood, forest fertilization often involves application of only N. Rates sometimes exceed 300 kg ha^{-1} of N. Application of a single nutrient such as N has the potential to create limitations of other nutrients and to aggravate existing nutrient limitations (Stalfelt 1972). Even if other nutrients are not limiting, but in marginal supply, the addition of a large amount of a single nutrient such as N may create deficiency (nutrient stress) of one or more of the other nutrients (Klemmedson and Ferguson 1973, Klemmedson and Tiedemann 1995).

The importance of adequate soil sulfur (S) for tree nutrition and growth has been documented in studies by Cochran (1978), Edmonds and Hsiang (1987) and Blake et al. (1990)). In the interior Pacific northwest, with some soils already shown to be deficient in S (Klock et al. 1971, Tiedemann and Berndt 1972, Tiedemann and Klock 1977),

© 1998 by the Northwest Scientific Association. All rights reserved.

fertilization with N has the potential to aggravate extant S deficiencies. Potassium (K) availability may also be adversely influenced by N fertilization (Mika et al. 1992).

The study site established by Mason et al. (1992), Waring et al. (1992) and Wickman et al. (1992) provided us an opportunity to examine effects of thinning and fertilization with 350 kg ha^{-1} of N as urea on concentrations of soil and forest floor nutrients five years after fertilization. We also wanted to determine if N fertilization at this rate influenced availabilities of phosphorus (P), S, or K after five years.

Methods

Description of the Study Area

A detailed description of the study area and rationale for treatments are found in Mason et al. (1992). Briefly, the study was conducted in a mixed conifer forest dominated by grand fir with scattered ponderosa pine (*Pinus ponderosa* Laws.) and Douglas-fir on the Malheur National Forest near Burns, Oregon. Elevation is approximately 1850 m. Annual precipitation is approximately 50 cm with most occurring as snowfall during the winter (Tiedemann and Higgins 1989). Soils are of the clayey, mixed, frigid family of Andic Xerochrepts and loamy-skeletal, mixed, frigid family of Lithic Argixerolls (Carlson 1974). These two soil types are intermixed throughout the study area. For both soil types, surface soils are gravelly or silt loams with pH from 5.6 to 6.5 that vary in depth from 15 to 30 cm with flat and angular rock fragments comprising 10 to 30%. Subsoils are gravelly or cobbly clay loam with pH 5.6 to 6.5, varying from 15 to 60 cm in thickness. Bedrock is hard basalt and andesite with tuffaceous interflow material (Carlson 1974). Understory vegetation in unthinned stands consisted mainly of small herbs of the Ericaceae and Orchidaceae families (Personal communication, Dr. Richard Waring, Professor, Forest Science, Oregon State University, Corvallis). Stand openings promoted development of bromegrass (*Bromus vulgaris* (Hook.) Shear) and shrubs such as rose (*Rosa gymnocarpa* Nutt.), pachistima (*Pachistima myrsinites* (Pursh) Raf.) and currant (*Ribes lacustre* (Pers.) Poir). Elk sedge (*Carex geyeri* Boott) and pinegrass (*Calamagrostis rubescens* Buckl.) were also common in both disturbed and undisturbed stands. Canadian and bull thistle (*Cirsium* spp.) were abundant in thinned stands.

Experimental Design and Treatments

Four square blocks, each 2.6 ha in size, were established on the study site. In summer 1984, a random one-half of each block was thinned to average tree spacing of 5.5 m. with emphasis on removal of trees smaller than 12.7 cm dbh for grand fir and 17.8 cm dbh for ponderosa pine. Trees were felled and left in place. In the fall of 1984, a random half of each thinned and unthinned plot was fertilized with 350 kg ha^{-1} of N as urea. This resulted in the following array of treatments on each of the four blocks:

1. Control (not thinned, not fertilized)
2. Not thinned, fertilized (NT-F)
3. Thinned, not fertilized (T-NF)
4. Thinned, fertilized (T-F)

Field Sampling

In late fall 1989, we collected forest floor and soil samples at 3 random locations on each plot of each block. Samples were collected at specified distances on a diagonal line across the plot from a random start with the plot corner as the random choice for starting point. At each location, forest floor samples were collected to mineral soil in a 400 cm^2 frame. No attempt was made to separate the forest floor into organic layers. Soils were collected at depths from 0-10 cm, 10-20 cm, and 20-30 cm with a bucket auger. No volume/weight measurements were taken. Samples were oven-dried to constant weight at 70°C. At each sample location, a bulk soil sample to 20 cm was collected for bioassay determination of nutrient availability. These samples were air-dried to constant weight in a well-ventilated greenhouse.

We did not measure forest floor depth or mass because this was beyond the scope of the experiment.

Chemical Analyses

Forest floor and soil samples for the three sample locations were composited by plot for each depth and analyzed for concentrations of total carbon (C), N, P, S, and K. Compositing samples enabled us to reduce costs for analyses. Compared

to single samples on each plot, compositing enabled us to incorporate point-to-point variability and, thus, to provide greater precision in estimate of plot means (Binkley and Vitousek 1989). Chemical analyses for forest floor and soils were as follows: total C by dry combustion using a high-frequency induction furnace (Nelson and Sommers 1982); total N by the Kjeldahl procedure (Bremner and Mulvaney 1982); total P on forest floor samples by magnesium nitrate dry ashing followed by vanadate-molybdate yellow color development (Chapman and Pratt 1961); total P for soils by hydrofluoric acid digest followed by ammonium molybdate-ascorbic acid color development (Bowman, 1988); total S was by dry combustion in a high-frequency induction furnace (Tiedemann and Anderson 1971); and total K by perchloric acid digestion followed by ICP spectroscopy (Barnes 1977).

Assessment of Nutrient Availability

A bioassay technique described by Jenny et al. (1950) was used to determine availabilities of N, P, S, and K using soil from each field treatment. 'Mica' barley (*Hordeum vulgare* L.) grown from certified seed was used as the test plant. The 3 field samples collected from each plot served as growth chamber replications. Soils were air-dried and sieved to pass a 2 mm screen. Each pot contained 400 g of soil. The following nutrient treatments were applied to the pots:

1. Check—no added nutrients
2. N_0—no nitrogen (P,K, and S added)
3. P_0—no phosphorus (N,K, and S added)
4. S_0—no sulfur (N,P, and K added)
5. K_0—no potassium (N,P, and S added)
6. Full—N,P,S, and K added

Nitrogen was added as ammonium nitrate (NH_4NO_3) at a rate equivalent to 300 kg ha^{-1} of N; phosphorus as calcium ortho-phosphate ($Ca(H_2PO_4)_2.H_2O$) at 200 kg ha^{-1} of P; sulfur as calcium sulfate ($CaSO_4.2H_2O$) at 100 kg ha^{-1} of S and potassium as potassium chloride (KCl) at 100 kg ha^{-1} of K;. Barley was grown for 16 weeks at alternating day-night temperatures of 24/18°C with a 12-hour day length. Lighting was provided by full spectrum fluorescent bulbs with wavelength emission comparable to that of sunlight. At the end of the trial, plants were harvested at the soil surface, oven-dried at 70°C to constant mass, and weighed.

We elected to use the bioassay test for nutrient availability, rather than chemical extraction, because we feel that it more accurately portrays availability of nutrients than does chemical extraction. Bioassay trials were originally developed by Mitscherlich, an early pioneer in soils research, before chemical testing was available. This type of test was refined by Jenny et al. (1950) and is an established means of assessing nutrient availability (Binkley and Vitousek 1989, Harrison and Helliwell 1979). Barley is not intended as a surrogate to indicate availability of nutrients to native tree species on the site—rather, it is a tool to assess availability of individual nutrients in the soil. We used barley as a test plant because of genetic uniformity and rapid growth rate whereby the entire soil mass is explored by plant roots during the 6 weeks of the test.

Statistical Analyses

The field design for the study was a split-plot analysis of variance in which thinning treatments were the major plots while fertilization treatments were the sub-plots. Differences among thinned and fertilized treatments for soil nutrient concentrations were analyzed using a split-split plot design with depths as the second split. Design for the forest floor statistical analysis was the same except there was no split for depth. A similar design was used for the bioassay trial except that the 3 field collection locations that served as growth chamber replicates were considered to be subsamples and growth chamber bioassay treatments were treated as another split in the analysis. Mean comparisons were made with the LSD test (Carmer and Swanson 1971). Unless otherwise indicated, significance level is $P<0.05$ for main effects and interactions in the ANOVA and for LSD means comparisons.

Results and Discussion

Concentrations of total C, N, and S from the control plots were higher in the forest floor than in soil (Table 1). Differences among soil depths were significant ($P<0.001$) for total C, N, and P. The soil depth X fertilizer/thinning treatment interaction was not significant for any constituent. Thus, depth relationships for soil nutrient data presented for the control plots are comparable to those for

TABLE 1. Concentrations (percent by weight) of total nutrients in forest floor and soil from the control treatment.

Constituent	Forest floor	Soil 0-10 cm	Soil 10-20 cm	Soil 20-30 cm
Total C	31.4[1]	1.94[a2]	1.03[b]	0.79[b]
Total N	0.71	0.09[a]	0.06[b]	0.05[b]
Total P	0.08	0.11[a]	0.09[ab]	0.06[b]
Total S	0.07	0.008[a]	0.008[a]	0.008[a]
Total K	0.20	0.27[a]	0.28[a]	0.27[a]

[1] Forest floor values were not compared statistically to soil values.

[2] Values for soil depths within an individual nutrient with the same lowercase letter are not significantly different at $P < 0.05$.

the treated plots. Total C in soils from the control plots declined from 1.94 % in the surface 0 to 10 cm to 0.79% in the 20 to 30 cm depth (Table 1). Total N and total P followed this same trend. Our values for total N are near the lower end of the range reported by Geist and Strickler (1978) for volcanic ash soils with mixed conifer vegetation and the depth relationships are similar. Total N and S values are also comparable to those of Tiedemann and Klock (1977) for a grand fir forest developed on recent volcanic ash. In those studies, it was concluded that soil N and S were deficient to the point that they would likely limit plant growth. That conclusion was reinforced by bioassay studies by Klock et al. (1971). It is likely, therefore, that N and S are both limiting at the present study site.

Forest Floor Nutrient Responses

Effects of thinning in the ANOVA were not significant for any measured nutrient constituent in the forest floor. This corresponds with results of Edmonds and Hsiang (1987) who compared N concentrations in forest floor of 35 thinned sites with that in 85 unthinned sites and found no significant difference.

Total N concentration of the forest floor was the only nutrient constituent influenced by fertilization, and the thinning X fertilization interaction was significant. Significantly higher N concentration in the NT-F treatment (0.92%) than in the other 3 treatments (0.71 to 0.77%) was responsible for the significant thinning X fertilization interaction (Table 2). Several interacting factors could account for higher N concentration in the forest floor of the NT-F treatment. Foliar N and litter N concentrations have both been shown to increase after fertilization (Turner 1977, Binkley and Reid 1985). Post-fertilization needle-fall

TABLE 2. Comparison of forest floor and soil nutrient concentrations (percent by weight) among thinned and fertilized treatments and the control. Soil nutrient values are the average of 0-10, 10-20, and 20-30 cm depths.

Constituent	Control	Not thinned, fertilized (NT-F)	Thinned, not fertilized (T-NF)	Thinned, fertilized (T-F)
		forest floor		
Total C	31.4[1]	34.7	32.1	33.1
Total N	0.71[a2]	0.92[b]	0.76[a]	0.77[a]
Total P	0.08	0.08	0.07	0.07
Total S	0.07	0.08	0.07	0.06
Total K	0.20	0.15	0.16	0.17
		soil		
Total C	1.26	1.56	1.40	1.47
Total N	0.07	0.07	0.08	0.08
Total P	0.09	0.08	0.08	0.08
Total S	0.008	0.008	0.008	0.008
Total K	0.27	0.27	0.34	0.30

[1] No comparison among means was made where the analysis of variance indicated that the main effect for thinning and fertilization treatments was not significant.

[2] Values with the same lowercase letter are not significantly different at $P < 0.05$.

would, thus, be expected to elevate litter (L or O_i) and, consequently, forest floor N concentrations. If this was a major factor responsible for greater N in the forest floor of NT-F treatment, we would have expected higher N concentrations with the T-F treatment as well. However, N concentrations with this treatment were the same as the control and the T-NF treatments. A more plausible explanation may be that the forest floor acts as a sink for applied nutrients as suggested by Fenn et al. (1991) where C/N ratios are large (C/N = 44 in the forest floor of our study). Up to 50% of applied N may be retained by the forest floor (Axellson 1985, Nason and Myrold 1992). Disturbance during thinning the T-F treatment may have reduced the effectiveness of the forest floor to retain fertilizer N and may explain the difference in total N concentration between this treatment and the NT-F treatment. Unfortunately, because we did not measure forest floor depth or mass, we cannot confirm this speculation.

Soil Nutrient Responses

There were no significant differences among thinned and fertilized treatments and the control (average of 3 soil depths) for soil total C, N, P, S, or K five years after fertilization (Table 2). Soil depths were averaged because the soil depth X fertilization/thinning treatment interaction was not significant for any nutrient.

Analysis of variance for bioassay of nutrient availability showed that differences among bioassay nutrient treatments and the interaction of bioassay nutrient treatments X fertilization/thinning treatments were highly significant ($P<0.001$ and $P<0.007$, respectively).

For thinning and fertilization treatments averaged, barley yields from the check treatment were significantly ($P<0.01$) less than the full nutrient treatment, indicating a deficiency of one or more nutrients (Table 3). Yields for N_0, S_0, and K_0 bioassay nutrient treatments were all significantly less ($P<0.01$) than yields of the full nutrient treatment indicating a possible deficiency of each of these nutrients (Table 3). There were no significant differences between the full nutrient treatment and P_0, indicating that P supply was sufficient. The severity of deficiency of N, S, and K can be evaluated using the "relative yield" concept of Jenny et al. (1950). Percent relative yield (RY) was determined by dividing the yield for individual treatments (i.e.,N_0) by the yield from the full nutrient treatment and multiplying by 100. Relative yield for N (19%) was considerably below the level (30%) that Jenny et al. (1950) indicate will yield a measurable response in the field to addition of N fertilizer (Table 3). The relative yield for S was also low (37%) but probably not at a level that a field response to fertilization would occur (Jenny et al. 1950). Even though K_0 yields were significantly less than the full nutrient treatment, relative yield of 85% suggests that availability of this nutrient was not limited.

TABLE 3. Barley yields (grams) and relative yields (percent) for 6 bioassay treatments averaged among thinning and fertilizer treatments.

Bioassay treatment					
Check	N_o	P_o	S_o	K_o	Full
0.774[a1]	0.836[a]	4.117[d]	1.601[b]	3.641[c]	4.300[d]
	Relative yield (RY)				
	19[2]	96	37	85	

[1] Values with the same lowercase letter are not significantly different at $P < 0.01$.

[2] Relative Yield (RY) = $\frac{\text{Yield for the } X_o \text{ Treatment}}{\text{Yield for the Full Treatment}} \times 100$

There were no significant differences in actual barley yields among field treatments for N_0, P_0, or K_0 (Table 4). Thus, it appears that high levels of urea-N fertilization did not have any effect on availabilities of those nutrients after 5 years. The decline of available N in soil from fertilized treatments to the same level as the control in 5 years supports results of Johnson et al. (1980). They found that within 161 days after urea fertilization at 200 kg ha^{-1}, soil mineral N levels (mostly ammonium-N) declined from 200 ppm to <10 ppm. Binkley (1986) also indicates that most soil N fertilization effects are short-lived. However, our results present a contrast to those of Binkley and Reid (1985) where N availability was twice as great in fertilized plots than unfertilized 18 years after application of ammonium nitrate.

Availability of S was influenced by N fertilization. Differences in S_0 yields among thinning and fertilization treatments were responsible for the bioassay treatment X field treatment interaction. Yield for S_0 from the NT-F field treatment was significantly less than yield for control and

TABLE 4. Barley yields (grams) for 6 bioassay treatments and 4 thinning and fertilizer field experiment treatments.

Field Experiment Treatment	Bioassay Treatment					
	Check	N_0	P_0	S_0	K_0	Full
Control	0.597[a1]	0.718[a]	4.104[a]	1.842[ab]	3.756[a]	4.058[a]
NT-F	0.708[a]	0.712[a]	4.255[a]	1.233[c]	3.494[a]	4.265[ab]
T-NF	0.913[a]	0.928[a]	4.039[a]	1.900[a]	3.444[a]	4.202[a]
T-F	0.876[a]	0.985[a]	4.074[a]	1.430[bc]	3.874[a]	4.673[b]

[1] Statistical comparisons are for differences among field experiment treatments for individual bioassay treatments. Values within a column with the same lowercase letter are not significantly different at $P < 0.05$.

T-NF treatments (Table 4). Barley yield from the S_0 bioassay treatment for the field T-F treatment was significantly less than yield for the T-NF treatment, but not significantly different from control or NT-F treatments. Tiedemann and Furniss (1985) observed a similar reduction in soil S availability under defoliated curlleaf cercocarpus (*Cercocarpus ledifolius* Nutt.) trees compared to undefoliated or lightly defoliated trees. In that study, they speculated that increased N and P in the litter layer resulting from deposition of insect frass increased demand for soil S by microbial populations, thereby reducing soil S availability.

Conclusions

Higher concentrations of total N in the forest floor of the NT-F treatment compared to the control leads us to conclude that there was a longer-term effect of fertilization on the forest floor. These differences suggest that the forest floor served as a sink for applied N. Results of Heilman et al. (1982), Axellson (1985) and Nason and Myrold (1992) support this conclusion.

There were no detectable differences in soil total N or available N between thinned and fertilized treatments and the control treatment. During the first year after fertilization at this same study site, Waring et al. (1992) measured substantially elevated levels of extracteable ammonium-N and nitrate-N in the upper 15 cm of soil. Plots of the NT-F and T-F treatments had 69 and 184 mg l^{-1} of extracteable N compared to 1.1 mg l^{-1} for the control treatment. Early growth responses of grand fir to fertilization were attributed to direct effects of increased soil N availability on numbers of primordia of overwintering buds and production of new needles (Waring et al. 1992). But, since N availability in fertilized treatments was the same as in the control treatment after 5 years, how do we account for increased radial growth of grand fir through the 5th year after fertilization measured by Wickman et al. (1992) on this same study area? Even longer-term tree growth responses (up to 15 years) have been observed in other studies (Miller and Tarrant 1983, Barclay and Brix 1985, Binkley 1986, Shoulders and Tiarks 1990). According to Brix (1983), longer-term growth response to fertilization is a result of improved growth efficiency (increased stem growth per unit leaf area) and increased leaf area. Turner (1977) observed increased foliage mass after fertilization of Douglas-fir in western Washington. On our study site, Wickman et al. (1992) measured increased foliage mass of new growth on trees from fertilized plots during the second through fifth years after fertilization. This likely accounts for the protracted radial growth response.

Although soil P and K availabilities were not affected by N fertilization, results clearly indicate a depression in soil S availability for the NT-F treatment when compared to control and T-NF treatments and for the T-F treatment compared to the T-NF treatment. The high level of N applied in the urea fertilization treatment apparently led to a deficiency of available S. Low inherent availability of soil S (RY = 37%) was probably a factor that contributed to the significant decline in bioassay yields that we observed. Results indicate that both N and S should be used in future fertilization efforts for sites where soil S concentrations are similar to those we observed (0.008%).

Acknowledgements

The authors appreciate technical reviews provided by Dr. Kermit Cromack, Jr., Professor of Forest Science, Oregon State University, Corvallis and

by Dr. James O. Klemmedson, Professor Emeritus, School of Renewable Natural Resources, University of Arizona, Tucson. We also thank Dr. H.N. Chappell, Potlatch Corp., and one anonymous reviewer for their helpful comments on the manuscript.

Literature Cited

Axellson, B. 1985. Increasing forest productivity and value by manipulating nutrient availability. *In* Forest potentials: productivity and value, Weyerhauser symposium, Weyerhauser Co. Pp. 5-37.

Barclay, H.J. and H. Brix. 1985. Fertilization and thinning effects on a Douglas-fir ecosystem at Shawnigan Lake: 12-year growth response. Canadian Forestry Service Information report BC-X-271, Pacific Forestry Centre, no location given. 33 p.

Barnes, R.M. 1977. Review of the applications of the inductively coupled plasma. *In* R.M. Barnes (Ed.) Applications of Inductively Coupled Plasma to Emission Spectroscopy. The Franklin Institute Press, Philadelphia, Penn. Pp. 3-49.

Binkley, D. 1986. Forest nutrition management. John Wiley and Sons, New York. 290 p.

Binkley, D. and P. Reid. 1985. Long-term increase of nitrogen availability from fertilization of Douglas-fir. Can. J. For. Res. 15:723-724.

Binkley, D. and P. Vitousek. 1989. Soil nutrient availability. *In* Pearcy, R.W., J.R. Ehleringer, H.A. Mooney, and P.W. Rundel. Plant Physiological Ecology. Field Methods and Instruments. Chapman and Hall, London. Pp. 75-96.

Blake, J.I., H.N. Chappell, W.S. Bennett, S.R. Webster, and S.P. Gessel. 1990. Douglas fir growth and foliar nutrient responses to nitrogen and sulfur fertilization. Soil Sci. Soc. Am. J. 54:257-262.

Bowman, R.A. 1988. A rapid method to determine total phosphorus in soils. Soil Sci. Soc. Am. J. 52:1301-1304.

Bremner, J.M. and C.S. Mulvaney. 1982. Total nitrogen. *In* Page, A.L. (Ed.), Methods of Soil Analysis, Part 2. Chemical and Microbiological Properties. 2nd ed., American Soc. of Agronomy, Madison, Wisc. Pp. 595-624.

Brix, H. 1983. Effects of thinning and nitrogen fertilization on growth of Douglas-fir: relative contribution of foliage quantity and efficiency. Can. J. For. Res. 13:167-175.

Carlson, G. 1974. Soil Resource Inventory Malheur National Forest. Basic Soil Information and Interpretive Tables. U.S. Department of Agriculture, Forest Service, Pacific Northwest Region, Portland, Oregon. 177 p.

Carmer, S.G. and M.R. Swanson. 1971. Detection of differences between means: A Monte Carlo Study of five pairwise multiple comparison procedures. Agron. J. 63:940-945.

Chapman, H.D. and P.F. Pratt. 1961. Methods of Analysis for Soils, Plants, and Waters. Univ. of California. Pp. 161-172.

Chappell, H.N., S.A.Y. Omule and S.P. Gessel. 1992. Fertilization in coastal northwest forests: using response information in developing stand-level tactics. *In* Chappell, H.N., G.F. Weetman, and R.E. Miller (Eds.). Forest Fertilization: Sustaining and Improving Nutrition and Growth of Western Forests. Institute of Forest Resources, Contrib. No. 73, College of Forest Resources, Univ. of Wash., Seattle. Pp. 98-113.

Cochran, P.H. 1978. Response of a pole-size ponderosa pine stand to nitrogen, phosphorus, and sulfur. U.S. Department of Agriculture, Forest Service Res. Note PNW-319. Pacific Northwest Forest and Range Exp. Sta., Portland, Oregon. 12 p.

Edmonds, R.L., and T. Hsiang. 1987. Forest floor and soil influence on response of Douglas-fir to urea. Soil Sci. Soc. Am. J. 50: 1332-1337.

Fenn, L.B., G.R. Gobran, and G.I. Agren. 1991. Nitrogen changes in forest litter after fertilization with calcium-urea. Soil Sci. Soc. Am. J. 55:509-514.

Geist, J.M. and G.S. Strickler. 1978. Physical and chemical properties of some Blue Mountain soils in northeast Oregon. U.S. Department of Agriculture, Forest Service Res. Pap. PNW-236. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon. 19 p.

Harrison, A.F. and D.R. Helliwell. 1979. A bioassay for comparing phosphorus availability in soils. J. Applied Ecology 16:497-505.

Heilman, P.E., T.H. Dao, H.H. Cheng, S.R. Webster, and L. Christensen. 1982. Comparison of fall and spring applications of ^{15}N-labeled urea to Douglas-fir: II. Fertilizer nitrogen recovery in trees and soil after 2 years. Soil Sci. Soc. Am. J. 46:1300-1304.

Jenny, H., J. Vlamis, and W.E. Martin. 1950. Greenhouse assay of fertility of California soils. Hilgardia 20 (1):1-9.

Johnson, D.W., N.T. Edwards, and D.E. Todd. 1980. Nitrogen mineralization, immobilization, and nitrification following urea fertilization of a forest soil under field and laboratory conditions. Soil Sci. Soc. Am. J. 44:610-616.

Klemmedson, J.O. and R.B. Ferguson. 1973. Effect of sulfur deficiency on yield and nitrogen content in bitterbrush (Purshia tridentata) seedlings on granitic soils. Soil Sci. Soc. Am. Proc. 37:947-951.

Klemmedson, J. O. and A.R. Tiedemann. 1995. Effects of nutrient stress. *In* Bedunah, D.J. and R.E. Sosebee, (Eds.) Wildland Plants: Physiological Ecology and Developmental Morphology. Society for Range Management, Denver, Colorado. Pp. 414-439.

Klock, G.O., J.M. Geist, and A.R. Tiedemann. 1971. Erosion control fertilization--from pot study to field testing. Sulphur Inst. J. 7(3):7-10.

Mason, R.R., B.E. Wickman, R.C. Beckwith, and H. G. Paul. 1992. Thinning and nitrogen fertilization in a grand fir stand infested with western spruce budworm: Part I: Insect response. For. Sci. 38:235-251.

Mika, P.G., J.A. Moore, R.P. Brockley, and R.F. Powers. 1992. Fertilization response by interior forests: when, where, and how much? *In* Chappell, H.N., G.F. Weetman, and R.E. Miller (Eds.). Forest fertilization: sustaining and improving nutrition and growth of western forests. Institute of Forest Resources, Contrib. No. 73, College of Forest Resources, Univ. of Wash., Seattle. Pp. 127-142.

Miller, R.E., J.R. Boyle, A.E. Harvey, T.M. Ballard, L.M. Palazzi, and R.F. Powers. 1992. Fertilizers and other means to maintain long-term productivity of western forests. *In* Chappell, H.N., G.F. Weetman, and R.E. Miller (Eds.). Forest Fertilization: Sustaining and Improving Nutrition and Growth of Western Forests. Institute of Forest Resources, Contrib. No. 73, College of Forest Resources, Univ. of Wash., Seattle. Pp. 203-222.

Miller, R.E. and R.F. Tarrant. 1983. Long-term growth response of Douglas-fir to ammonium nitrate fertilizer. For. Sci. 29:127-137.

Moore, J.A. 1988. Response of Douglas-fir, grand fir, and western white pine to forest fertilization. *In* Schmidt, W.C. (Comp.), Proceedings—Future Forests of the Mountain West: a Stand Culture Symposium, Sept. 29 to Oct. 3, 1986, Missoula, Mt. U.S. Department of Agriculture, Forest Service Gen. Tech. Rep. INT-243. Intermountain Research Station, Ogden, Utah. Pp. 226-230.

Nason, G.E. and D.D. Myrold. 1992. Nitrogen fertilizers: fates and environmental effects in forests. *In* Chappell, H.N., G.F. Weetman, and R.E. Miller (Eds.). Forest Fertilization: Sustaining and Improving Nutrition and Growth of Western Forests. Institute of Forest Resources, Contrib. No. 73, College of Forest Resources, Univ. of Wash., Seattle. Pp. 67-81.

Received 29 October 1997
Accepted for publication 7 March 1998

Nelson, W.W. and L.E. Sommers. 1982. Total carbon, organic carbon, and organic matter. *In* Page, A.L. (Ed.), Methods of Soil Analysis, Part 2. Chemical and Microbiological Properties. 2nd ed., American Soc. of Agronomy, Madison, Wisc. Pp. 539-579.

Peterson, C.E. and J.W. Hazard. 1990. Regional variation in growth response of coastal Douglas-fir to nitrogen fertilizer in the Pacific Northwest. For. Sci. 36:625-640.

Shoulders, E. and A.E. Tiarks. 1990. Nine-year response of thinned slash pine to nitrogen, phosphorus, and potassium. Soil Sci. Soc. Am. J. 54:234-237.

Stalfelt, M.G. 1972. Stalfelt's Plant Ecology. (English translation, Longman Group Limited), John Wiley and Sons (Halsted Press), NY. 592 p.

Tiedemann, A.R. and T.D. Anderson. 1971. Rapid analysis of total sulphur is soils and plant material. Plant and Soil 35:197-200.

Tiedemann, A.R. and H.W. Berndt. 1972. Vegetation and soils of a 30-year deer and elk exclosure in central Washington. Northwest Sci. 46: 59-66.

Tiedemann, A.R. and G.O. Klock. 1977. Meeks table research natural area--reference sampling and habitat classification. U.S. Department of Agriculture, Forest Service Res. Pap. PNW-223. Pacific Northwest Forest and Range Exp. Sta., Portland, Oregon. 19 Pp.

Tiedemann, A.R. and M.M. Furniss. 1985. Soil and litter nutrient responses to looper defoliation of curlleaf mountain mahogany. For. Sci. 31:382-388.

Tiedemann, A.R. and D.A. Higgins. 1989. Effects of management strategies on water resources. *In* Quigley, T.M., H.R. Sanderson, and A.R. Tiedemann. Managing Interior Northwest Rangelands: the Oregon Range Evaluation Project. U.S. Department of Agriculture, Forest Service Gen. Tech. Rep. PNW-GTR-238. Pacific Northwest Res. Sta., Portland, Oreg. Pp. 57-91.

Turner, John. 1977. Effect of nitrogen availability on nitrogen cycling in a Douglas-fir stand. For. Sci. 23:307-316.

Waring, R.H., T. Savage, K. Cromack, Jr., and C. Rose. 1992. Thinning and nitrogen fertilization in a grand fir stand infested with western spruce budworm. Part IV: an ecosystem management perspective. For. Sci. 38:275-286.

Wickman, B.E., R.R. Mason, and H.G. Paul. 1992. Thinning and nitrogen fertilization in a grand fir stand infested with western spruce budworm. Part II: Tree growth response. For. Sci. 38:252-264.

Joseph W. Witt,[1] Roseburg District, Bureau of Land Management, U. S. Department of the Interior, 777 N. W. Garden Valley Boulevard, Roseburg, Oregon 97470

Distribution of the Marbled Murrelet in Southwestern Oregon

Abstract

I summarized data from 889 intensive 2-hour morning surveys between 1992 and 1997 to determine the distribution of marbled murrelets (*Brachyramphus marmoratus*) in suitable habitat (mature and old-growth forest stands) on the Roseburg District of Bureau of Land Management in southwestern Oregon. Murrelets were detected on 17 surveys at 6 sites. Three sites were considered occupied, as defined by the Pacific Seabird Group (PSG), Marbled Murrelet Technical Committee guidelines (Ralph et al. 1993; 1994), all were less than 59 km from the coast. The farthest inland site with detections was 61 km from the coast. Two potential variables are discussed, which may influence the patterns of distribution and abundance in the study area: energetics and predation. Using the PSG protocols, surveys in southwestern Oregon should be conducted in all suitable habitat located 60 km inland from the coast rather than the guidelines for 80 km.

Introduction

The Marbled Murrelet (*Brachyramphus marmoratus*) is a dove-sized seabird in the Alcidae family. The murrelet distribution is closely associated with older-age coniferous forests in the Pacific Northwest (Sealy and Carter 1984; Carter and Sealy 1987; Hamer 1995; Hamer and Nelson 1995; Miller and Ralph 1995). Habitat used by murrelets for nesting usually has large-diameter trees, highly variable canopy closure (15%-100%), and a high number of potential nesting platforms (Grenier and Nelson 1995, Hamer and Nelson 1995). The marbled murrelet was listed in 1992 as a federal threatened species in Washington, Oregon, and California (U.S. Fish and Wildlife Service 1992).

On federal lands, any proposed action that modifies suitable murrelet habitat or impacts the murrelet's ability to reproduce requires the managing agency to initiate intensive surveys based upon Pacific Seabird Group (PSG), Marbled Murrelet Technical Committee guidelines, before implementing the proposed action; thereby, complying with the regulatory rules and regulations of the Endangered Species Act of 1973. The guidelines suggest that all actions within 80 km of the ocean be examined for murrelets and, if occupied, managed appropriately. In Washington the farthest known inland occupied site is 84 km from the coast (Hamer 1995), and in Oregon and California the sites are 61 and 56 km, respectively (U. S. Fish and Wildlife Service 1994). In southwestern Oregon, Dillingham et al. (1995) examined the distribution of the murrelets in the Siskiyou National Forest and suggested their distribution was correlated to vegetation type. In the Siskiyou National Forest murrelets have been found as far as 42 km inland (S.K. Nelson, unpubl. data; P.W. Paton unpubl data). With similar information needs, the Roseburg District of the Bureau of Land Management in the south Coast Range, examined the distribution of the marbled murrelet between 1992 and 1997 by conducting intensive surveys. This paper summarizes our murrelet survey effort and discusses potential factors that may affect murrelet distribution in southwestern Oregon.

Methods

The study area was located west of Roseburg, Oregon (see Fig. 1), approximately 45 to 80 km from the Oregon coast. The land ownership pattern on the study area consists of a checkerboard arrangement of alternating square mile (2.59 km^2) sections of federal and non-federal lands (Richardson 1980). Federal lands, administered by the Roseburg District of the Bureau of Land Management (BLM), have not been as extensively harvested as non-federal lands. I estimated that approximately 6% of non-federal forested stands were ≥80 years old based on aerial photo interpretation, and half the lands administered by the District were still covered by older forests and dominated by trees ≥120 years old (USDI). The BLM lands typically include a mixture of young forests and older unlogged forests (80-450 years

[1]Current Address: Mason Neck N.W.R., 14344 Jefferson Davis Hwy., Woodbridge, VA 22191

© 1998 by the Northwest Scientific Association. All rights reserved.

old) and recent clearcuts. The majority of the young forests, less than 50 years old, were regenerated after logging.

The study area is in the western hemlock (*Tsuga heterophylla*) vegetation zone (Franklin and Dyrness 1973), an area dominated by temperate coniferous forests of Douglas-fir (*Pseudotsuga menziesii*) and western hemlock. This region is characterized by mild, wet winters and warm, dry summers. The vegetation in the study area was classified as either suitable or nonsuitable based upon aerial photographs, forest inventory data, and on-site examinations of the stands. I use the term suitable habitat to mean any forest stand having a medium-to-large live tree and snag (diameter at breast height >38 cm) components in the overstory and were equal to or greater than 80 years of age, and nonsuitable habitat to mean any forest stand less than 80 years of age having small-to-medium live tree (diameter at breast height <38 cm) components in the overstory.

Surveys were conducted between 1992 and 1997 for the dual purpose of examining the overall distribution of the murrelet on Bureau lands and inventorying potential timber sale areas. One hundred and five intensive inventory sites were established in suitable habitat during the study on federal lands (46 km to 74 km from the coast), with 64% (n=67) of the sites established specifically to examine the overall distribution of the murrelets and not associated with any planned timber harvest activities (Fig. 1). Whereas, planned timber harvest activities and their associated survey sites (n=38) were grouped and located in areas designated for intense timber management (Northwest Forest Plan, USDA et al. 1994), which systematically avoids large blocks of suitable habitat for the northern spotted owl (*Strix occidentalis*) and the marbled murrelet.

Site location of the non-timber related inventory sites were based upon a non-random selection process, whereby they were systematically and evenly distributed across the breadth of the study area and between timber harvesting activity centers to obtain an equitable and representative sample. A random selection of sites in suitable habitat would have clumped the survey locations in the late-successional reserve management areas for the marbled murrelet and northern spotted owl (*Strix occidentalis caurina*), as these areas are prominent features on the landscape and contain the majority of the suitable murrelet habitat. Conservation reserve areas (designed to maintain a viable population of spotted owls in western Oregon) are not randomly distributed. Their clumped distribution is the result of ownership patterns and historical harvesting activities in the study area.

Once a general location or survey area was selected, individual stand selection was based upon the best available stand of suitable habitat (that is, the stands were older, contained the largest diameter conifers, and potentially the greatest nesting platform availability - Burger 1995; Grenier and Nelson 1995; Hamer 1995; and Hamer and Nelson 1995), largest patch size (that is, the larger the mean patch size the better - Raphael et al. 1995), stands that were not impacted by salvage logging, and were safely accessible. This sampling procedure was designed to distribute the inventory sites in a manner whereby the overall distribution of the species in a range of distances from the coast could be examined. At each survey site a range of 1 to 7 survey stations (mean = 3.6) were established. The number of stations per survey site reflected the size of the site. In general, one survey station was established for each 10 ha of suitable habitat.

Murrelet surveys were systematically located and conducted from 1 May to 5 August, using the intensive (fixed station) survey protocol and station guidelines suggested by the Pacific Seabird Group (PSG), Marbled Murrelet Technical Committee guides (1992-1994, Redwood Sciences Laboratory, 1700 Bayview Drive, Arcata, CA, unpubl. reps.). Each site was visited a minimum of four times per year during the survey period, with at least two visits conducted at each site after June 20 and one visit during the peak period of activity (last three weeks of July). At each station throughout the survey season, surveys were conducted during a 2-hour period from 45 min before to 75 min after official sunrise. During the study, surveys at each site were conducted for two consecutive years, except for 15 new survey sites (4 for general distribution and 11 for timber related activities) established in 1997. The patterns of activity were quantified based on the visual and auditory detections at the sites, and the definitions proposed by Paton (1995). In addition, all sites with detections had additional visits above protocol minimums to either verify or determine potential occupation and nesting.

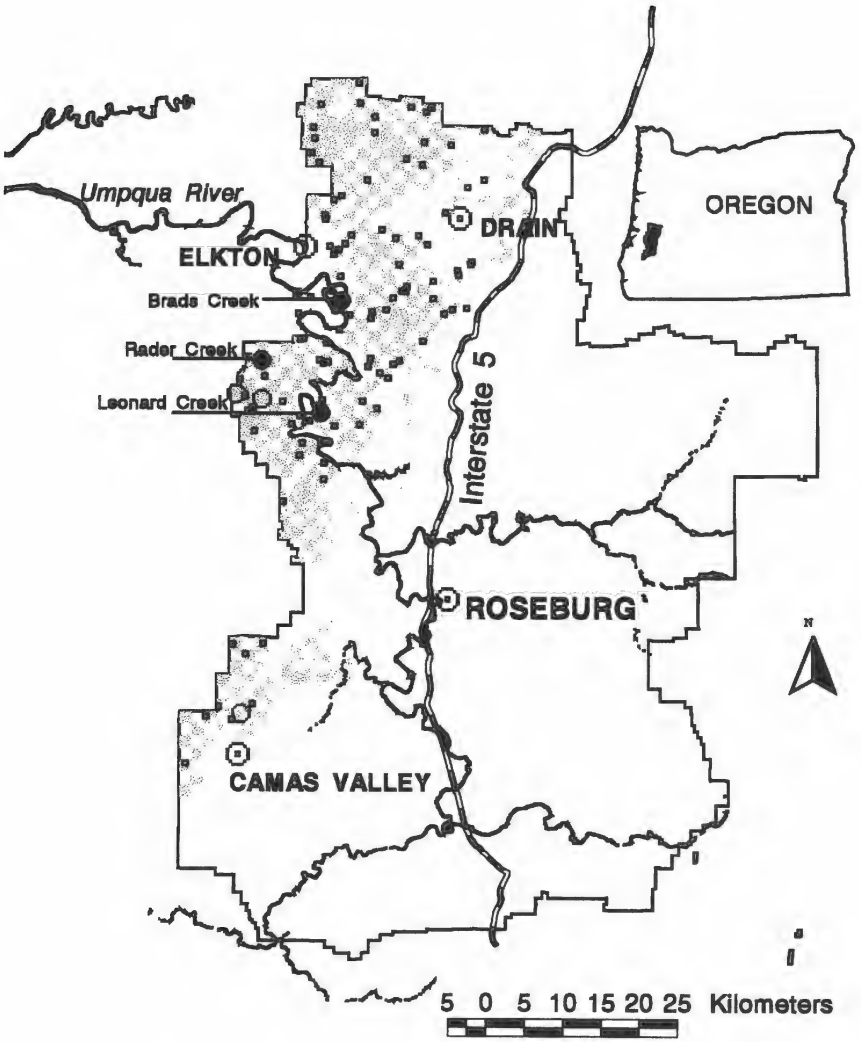


Figure 1. Distribution of intensive survey sites (solid squares), occupied sites (solid circles), and sites with detections only (hollow circles) on public lands in the Roseburg District of Bureau of Land Management in southwestern Oregon. The shaded area represents Bureau administered lands within the study area and dotted circles human population centers.

Surveyors had their hearing tested on one or more occasions during the study, and were trained each year for a minimum of two weeks during the month of April to familiarize them with both auditory and visual identification of murrelets and all potential birds that could be seen or heard during a survey.

Results

Between 1992 and 1997, we conducted 889 intensive (fixed station) 2-hr surveys. Murrelets were detected at six sites during 17 of these surveys. Subcanopy and circling flight behaviors were observed at three sites (Rader Creek, Leonard

Creek, and Brads Creek) and, therefore, were considered occupied as defined by the Pacific Seabird Group, Marbled Murrelet Technical Committee guides and Paton (1995). At the other three sites, murrelets were detected flying above the canopy only. At two of these sites there were numerous detections each with multiple keer calls (a two-syllable, high pitched vocalization, similar to the vocalizations of many gulls, *Larus* spp., [O'Donnell 1993]) per detection during two separate surveys to each site. The third site had only two single auditory detections (i.e., two single 'keer' calls above the canopy) within two minutes of each other during the second year of survey. No detections were observed during an additional third year of survey effort.

The Leonard Creek site adjacent to the Umpqua River was initially found in 1992 and was periodically occupied (unoccupied in 1994 and 1996 based on the lack of detections) during the study. The Rader Creek site was found in 1993 and has been consistently occupied. With additional visits to Rader Creek in 1994, the farthest known inland nest site was identified and characterized (Witt, In press). The Brads Creek site, also adjacent to the Umpqua River, was found in 1995 and was only unoccupied in 1996.

The murrelet flight paths observed at Rader Creek site indicate the use of creeks and drainages to get to and from the site. While the observations at Leonard Creek suggest a more directional east and west line of flight, as they were seen using road prisms and not the adjacent Umpqua River. The two sites with above canopy detections near Rader Creek also suggest a east and west line of flight.

The mean shortest distance to the Oregon coast for all survey sites was 59.4 km (S.D.= 6.8) with a range of 46 km to 74 km. All three occupied sites were less than 59 km from the coast (range: 49-58 km). Two of the three sites with above canopy detections only were located only a few kilometers from the Rader Creek site and were 46 km and 50 km from the coast. The farthest inland site with two above canopy detections was 61 km from the coast.

Discussion

The sampling approach used in the study combined the need for survey clearance efforts for potential timber sale projects with the basic need for information about the murrelet distribution in western Oregon. The systematic design incorporated a variety of factors (availability of suitable habitat on public lands, quality of suitable habitat, patch size, and distance to coast) in an effort to achieve a representative sample of the potential habitat available in the District and the Coast Range.

Miller and Ralph (1995) in California found that the strongest predictors of murrelet presence and occupancy in California were the density of old-growth cover and species composition, with mean detection rates being highest in major drainages and at lower elevations. They also found a strong pattern of declining presence with increased distance from the coast, with the highest frequencies of presence (89%) at stands within 10 km of the coast. In Washington, an analysis of landscape attributes indicated that the amount (mean patch size) and configuration (mean shape index) of the old-growth and large sawtimber stands were important factors in murrelet distribution (Raphael et al. 1995). In a vegetation analysis, Hamer (1995) found a pattern related to the distance from the coast, with 98.5% of all detections being observed <64 km inland.

In Oregon, murrelets were found to have a clumped distribution along the coast and in the adjacent Coast Range, with concentrations between Yaquina and Heceta heads (Nelson et al. 1992). Grenier and Nelson (1995) compared occupied sites with random locations and found that occupied sites were generally older, had larger midstory trees, and had larger and greater densities of dominant trees than random sites. Dillingham et al.(1995) hypothesized that the murrelet distribution in the Siskiyou National Forest in southwestern Oregon was influenced by habitat suitability, vegetation type, topography, climate, and distance from the ocean. Within the tanoak/western hemlock zone they observed 448 detections and only one detection was observed in the eastern part of the national forest in the mixed conifer/mixed evergreen zone. The mixed conifer/mixed evergreen zone was suspected to limit murrelet distribution because it was drier and had smaller trees than the western hemlock vegetation zone (Dillingham et al. 1995).

The distribution pattern observed in California and Washington of declining presence with increased distance from the coast suggest that some

form of limiting factor is acting on the murrelet. Dillingham et al. (1995) hypothesized that the limiting factor was related to tree growth and abundance of large limbs. In the Roseburg study area, I believe that both the physical and climatic factors in the study area are conducive to creating suitable nesting habitat. One possible reason for their present distribution and low numbers in the study area is that the population is already drastically limited and the pattern observed is merely a reflection of a decreasing population, where only the optimal or best habitat is occupied by the few remaining individuals. The Rader Creek nest site would fit this profile as it is both one of the oldest and one of the largest patches in the study area. The other two sites are not exceptionaly old and they are relatively small in size, but because they are adjacent to the Umpqua River may be more influenced by the presence of early morning fog along the river.

Perhaps it is a combination of factors that formed the patterns I observed. I believe that energetic requirements of flying inland to incubate eggs and feed young, and coupled with increased opportunties of being predated while in transit could have a major influence on their distribution and abundance inland. Another factor would be the potential predation of fledglings heading to the ocean and their potential navigational problems or exhaustion while on route (Nelson and Hamer 1995). Eberl and Picman (1993) found that the reproductive success and density of red-throated loons (*Gavia stellata*) decreased as the distance to the ocean increased. Although, both energetics and predation have not been formally tested, numerous authors have suggested that both aspects could influence the overall inland distribution of marbled murrelets (Dillingham et al. 1995; Hamer 1995; Hamer and Nelson 1995; Nelson and Hamer 1995; Ralph et al. 1995).

In conclusion, I agree with Ralph et al. (1995) and consider it prudent to focus survey efforts in the recovery zones, and that there is little virtue in conducting surveys in areas where murrelets are rarely observed. Given the present knowledge of the distribution and the ecology of the marbled murrelet, I recommend that surveys in southwestern Oregon be conducted in all suitable habitat located 60 km inland from the coast using the Pacific Seabird Group, Marbled Murrelet Technical Committee guides (Ralph et al. 1993; 1994) rather than the guidelines for 80 km.

Acknowledgements

We are grateful to A.E. Burns, P. A. Burns, E. I. Gayner, R. O. Harper, S. W. Hoefs, A. K. Hubbard, E. K. Karnatz, E. T. Scheuering, G. L. Slater, R. J. Straub, and S. A. Wolfe for their capable and enthusiastic assistance in the field. We thank Joseph B. Lint for his helpful comments on earlier drafts of this manuscript.

Literature Cited

Burger, A. E. 1995. Inland habitat associations of marbled murrelets in British Columbia, pp. 151-161. In: C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt (eds.), Ecology and conservation of the marbled murrelet in North America. USDA For. Serv. Gen. Tech. Rep. PSW-GTR-152.

Carter, H. R. and S. G. Sealy. 1987. Inland records of downy young and fledgling marbled murrelets in North America. Murrelet 68: 58-63.

Dillingham, C. P., R. C. Miller, and L. O. Webb. 1995. Marbled murrelet distribution in the Siskiyou National Forest of southwestern Oregon. In: S. K. Nelson and S. G. Sealy (eds.). Biology of the marbled murrelet: inland and at sea. Northwest. Nat. 76: 33-39.

Eberl, C., and J. Picman. 1993. Effect of nest-site location on reproductive success of red-throated loons (*Gavia stellata*. Auk 110:436-444.

Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8. 417 pp.

Grenier, J. J. and S. K. Nelson. 1995. Marbled murrelet habitat associations in Oregon, pp. 191-204. In: C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt (eds.), Ecology and conservation of the marbled murrelet in North America. USDA For. Serv. Gen. Tech. Rep. PSW-GTR-152.

Hamer, T. E. 1995. Inland habitat association of marbled murrelets in western Washington, pp. 163-176. In: C. J. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt (eds.), Ecology and conservation of the marbled murrelet in North America. USDA For. Serv. Gen. Tech. Rep. PSW- GTR-152.

Hamer, T. E. and S. K. Nelson. 1995. Characteristics of marbled murrelet nest trees and nesting stands, pp. 69- 82. In: C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt (eds.), Ecology and conservation of the marbled murrelet in North America. USDA For. Serv. Gen. Tech. Rep. PSW-GTR-152.

Miller, S. L. and C. J. Ralph. 1995. Relationship of marbled murrelet with habitat characteristics at inland sites in California, pp 205-215. In: C. J. Ralph, G. L. Hunt,

Jr., M. G. Raphael, and J. F. Piatt (eds.), Ecology and conservation of the marbled murrelet in North America. USDA For. Serv. Gen. Tech. Rep. PSW- GTR-152.

Nelson, S. K., M. L. C. McAllister, M. A. Stern, D. H. Varoujean, and J. M. Scott. 1992. The marbled murrelet in Oregon, 1899-1987, pp. 61-91. In: H. R. Carter, and M. L. Proc. West. Found. Vert. Zool. 5.

O'Donnell, B. 1993. Patterns of activity and vocalizations of the Marbled Murrelet, *Brachyramphus marmoratus*, within old-growth redwood stands in northwestern California. Arcata, CA: Humboldt State University; 84 p. M. Sc. Thesis.

Paton, P. W, C. 1995. Marbled murrelet inland patterns of activity: defining detections and behavior, pp. 113-116. In: C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt (eds.), Ecology and conservation of the marbled murrelet in North America. USDA For. Serv. Gen. Tech. Rep. PSW-GTR-152.

Paton, P. W. C. and C. J. Ralph. 1990. Distribution of the marbled murrelet at inland sites in California. Norhtwest. Nat. 71:72-84.

Ralph, C. J., S. K. Nelson, M. M. Shaughnessy, and S. L. Miller. 1993. Methods for surveying marbled murrelet in forests. Technical paper #1. Corvallis, OR: Oregon Cooperative Wildlife Research Unit, Oregon State University, Corvallis, OR; 48p.

Ralph, C. J., S. K. Nelson, M. M. Shaughnessy, S. L. Miller, and T. E. Hamer. 1994. Methods for surveying marbled murrelet in forests. Technical paper #1, revision. Corvallis, OR: Oregon Cooperative Wildlife Research Unit, Oregon State University, Corvallis, OR; 48p.

Received 21 August 1997
Accepted for publication 26 January 1998

Raphael, M. G., J. A. Young, and B. M. Galleher. 1995. A landscape-level analysis of marbled murrelet habitat in western Washington, pp. 177-189. In: C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt (eds.), Ecology and conservation of the marbled murrelet in North America. USDA For. Serv. Gen. Tech. Rep. PSW- GTR-152.

Rodway, M. S. 1990. Status report on the marbled murrelet, Brachyramphus marmoratus, in Canada. Ottawa: Committee on the Status of Endangered Wildlife in Canada.

Sealy, S. G. and H. R. Carter. 1984. At-sea distribution and nesting habitat of the marbled murrelet in British Columbia: problems in the conservation of a solitarily nesting seabird, pp. 737-756. In: J. P. Croxall, P. G. H. Evans, and R. W. Schreiber (eds.), Status and conservation of the world's seabirds. ICBP Tech. Publ. No. 2.

U. S. Department of Agriculture/U. S. Department of the Interior. 1994. Supplemental environmental impact statement on management of habitat for late- successional and old-growth forest related species within the range of the Northern Spotted Owl. Portland, OR.

U. S. Fish and Wildlife Service. 1992. Endangered and threatened wildlife and plants: determination of threatened status for the Washington, Oregon, and California population of the marbled murrelet.

USDI Fish and Wildl. Serv. Fed. Reg. 57:45328-45337. U.S. Fish and Wildlife Service. 1994. Endangered and threatened wildlife and plants: proposed designation of critical habitat for the marbled murrelet. USDI Fish and Wildl. Serv. Fed. Reg. 59:3811-3823.

Witt, J. W. In press. Notes on the activity and characteristics of an inland marbled murrelet nest site in Douglas County, Oregon. Northwest. Nat. 79(1).

Nobuya Suzuki, Department of Forest Science, Oregon State University, 020 Forestry Sciences Laboratory, Corvallis, Oregon 97331

William C. McComb, Department of Forestry and Wildlife Management, University of Massachusetts, Amherst, Massachusetts 01003

Habitat Classification Models for Beaver (*Castor canadensis*) in the Streams of the Central Oregon Coast Range

Abstract

During 1988-1989, 22 stream habitat attributes were measured and compared between 40 beaver-dam sites and 72 unoccupied-stream sites to identify attributes associated with dam-site selection by beaver (*Castor canadensis*) in streams of the Drift Creek Basin, Lincoln County, Oregon. Beaver built dams in areas with wide valley-floors; narrow, low gradient streams; high grass/sedge cover; and low red alder (*Alnus rubra*) and shrub cover. Unoccupied sites lacked these characteristics. A discriminant function model correctly classified 83% of beaver-dam sites and 88% of unoccupied-stream sites with a chance-corrected classification rate of 69% (Cohen's *Kappa* statistic). We used 3 geomorphic attributes (stream width, gradient, and valley floor width) and developed a new Habitat Suitability Index (HSI) model for the basin. Land managers can use the discriminant function model or the HSI model to inventory potential beaver-dam sites along streams of the Oregon Coast Range. Information obtained from our habitat classification models can be incorporated into plans to preserve unique riparian habitats maintained by beaver.

Introduction

Over 60 million beaver (*Castor canadensis*) are estimated to have inhabited rivers, streams, and lakes of North America (Seton 1929). Prior to settlement by Europeans, drainage systems, which supported these large beaver populations, were characterized by having multiple main channels braided with numerous small side channels and sloughs (Sedell and Froggatt 1984). Following settlement, fur trappers exploited beaver populations to near extinction by 1900 (Anderson 1964). Subsequently, human activities drastically altered the ecological characteristics of streams and rivers. Stream cleanings removed in-stream structures, such as large woody debris and boulders, from channels to secure navigation on rivers and simplified complex channel structures (Sedell and Froggatt 1984). As a result, many small side-channels and sloughs, which once were occupied by numerous beaver colonies, have disappeared from large streams and rivers (Sedell and Froggatt 1984). In recent years, population management and reintroduction efforts have brought beaver populations back to 6-12 million individuals in North America (Anderson 1964, Brayton 1984, Apple 1985, Naiman et al. 1988). Characteristics of stream geomorphology and hydrology, and the distribution of suitable beaver habitats in the modern drainage systems, have become quite different from those in the pre-settlement systems. In mountain streams of the Oregon Coast Range, beaver dams are now more commonly found in small, lower-order tributaries than in large channels within the drainage systems. A recent estimate indicates that there are approximately 70,000 beaver in Oregon of which half occur in these coastal streams (Guthrie and Sedell 1988).

To evaluate habitat suitability for beaver, various habitat classification models have been developed (Slough and Sadleir 1977, Allen 1983, Howard and Larson 1985, Beier and Barrett 1987). Among these models, the U.S. Fish and Wildlife Service developed a Habitat Suitability Index (HSI) model that was potentially applicable throughout the range of the beaver (Allen 1983). Despite its wide geographical scope, the U.S. Fish and Wildlife HSI model was not sensitive enough to accommodate variability in local conditions of the Oregon Coast Range, and it classified an unusually high proportion (78%) of beaver-unoccupied sites as optimal habitats (Suzuki 1992).

To our knowledge, no habitat classification models have been developed for the streams of the Oregon Coast Range, and none of the existing

© 1998 by the Northwest Scientific Association. All rights reserved.

models are applicable in the region. Our objectives were: 1) to describe the distribution and abundance of beaver dams in the Drift Creek Basin of the Oregon Coast Range, 2) to describe habitat variables associated with beaver dams in the basin, and 3) to develop habitat classification models for beaver that identify stream reaches potentially suitable for beaver dam sites within the basin.

Study Area and Methods

The Drift Creek Basin is located in the western slope of the central Oregon Coast Range, Lincoln County, Oregon (Figure 1). Drift Creek and its tributaries drain 179 km^2 in area, and elevation of the drainage ranges from sea level to 860 m. Red alder (*Alnus rubra*) and Douglas-fir (*Pseudotsuga menziesii*) were the most common tree species found throughout the area. Other tree species included western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), and bigleaf maple (*Acer macrophyllum*). Salmonberry (*Rubus spectabilis*) was the dominant understory-shrub species. Other understory vegetation included vine maple (*A. circinatum*), elderberry (*Sambucus racemosa*), thimbleberry (*R. parviflorus*), stinking currant (*Ribes bracteosm*), California hazel (*Corylus cornuta*), huckleberry (*Vaccinium parvifolium*), devil's-club (*Oplopanax horridum*), western swordfern (*Polystichum munitum*), sedges (*Carex* spp.), and various forbs and grasses.

In the fall of 1988 and 1989, we surveyed streams of the Drift Creek Basin on foot and located beaver dams on topographic maps (scale 1:24000). Surveys conducted by fisheries scientists

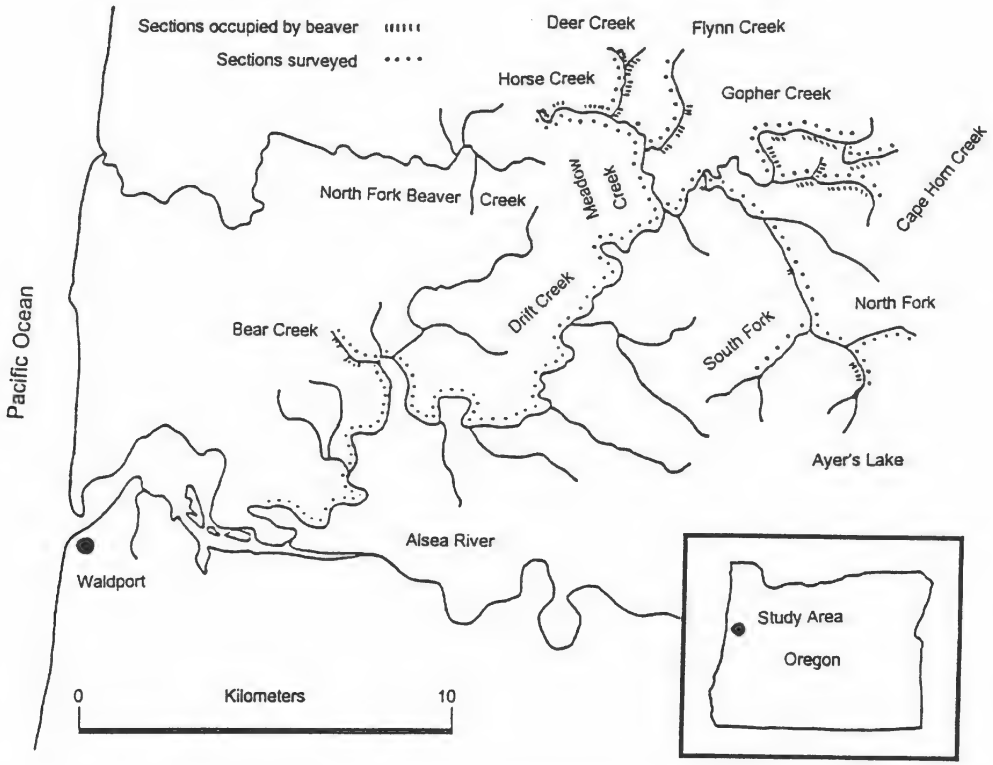


Figure 1. Location of the Drift Creek Basin and map showing the stream section surveyed and the stream section occupied by beaver, Lincoln County, Oregon, 1988-1989.

in the summer of 1988 and 1989 provided additional locations of beaver dams and measurements of channel geomorphology in other streams in the basin (Schwartz 1991). Based on beaver dam locations, each stream was divided into beaver-occupied and beaver-unoccupied sections (Figure 1). Beaver-occupied sections were characterized by presence of dams and ponds that were actively maintained by beavers. Unoccupied sections were stream sections without beaver dams; however, these sections might be occupied by bank-dwelling beavers.

We conducted a habitat survey at 40 randomly selected beaver dam sites within the beaver-occupied sections and 72 randomly selected points within the beaver-unoccupied sections of streams. Because very few dams were found on the 4th-order and 5th-order sections of Drift Creek, all sampling points for habitat survey were selected in 1st- to 3rd-order streams. Twenty-two variables, which represent channel geomorphology, cover by vegetative layers, and cover by shrubs and tree species, were measured during the survey (Table 2, Suzuki 1992). We measured stream width and valley-floor width with a meter tape and stream depth with a measuring stick. Measurements of stream width and depth reflected the bank-full dimensions of channels. At each beaver dam-site, stream width and depth were measured at a point immediately downstream from the dam. Thus, the measurement reflected the original channel characteristics. Valley-floor width was measured to reflect the width of a 100-year flood plain. Stream gradient was measured by sighting a clinometer over the distance of 20-m upstream and 20-m downstream from a sampling point, and the average gradient was calculated for each site. We used a clinometer and measured the angle of bank slope over the distance of 20 m upslope from the channel center. The average slope of banks on both sides of the stream was calculated for each site. Vegetative variables were ocularly estimated within a 20-m radius plot and within a nested 10-m radius plot. These plots were centered on a randomly assigned stream bank. Percent cover of trees and shrubs was estimated within the 20-m radius plot, and percent cover of herbaceous vegetation (grass/sedge, forb, and fern) was estimated within a nested 10-m radius plot.

Habitat variables were examined for normality by normal-probability plot and W, the Shapiro-Wilk statistic (SAS Institute Inc. 1990:627). Logarithmic and square root transformations were attempted on all non-normal variables. Either original or transformed variables with near normal distributions were compared between dam sites and unoccupied sites with Student's t-tests (SAS Institute Inc. 1989:1633). Non-normal variables, which could not be transformed ($W < 0.7$), were compared between dam sites and unoccupied sites with Wilcoxon rank-sum tests (SAS Institute Inc. 1989:1198).

We used stepwise discriminant analysis to select a combination of variables which best separated dam sites from unoccupied sites (SAS Institute Inc. 1989:1493). The variable selection did not rely on the results of the t-tests. Linear correlations between all possible pairs of the variables were examined with Pearson's correlation coefficient (Devore and Peck 1986:113). Multicollinearity among the variables was reduced by testing correlated variables ($r > 0.6$) separately in a stepwise discriminant analysis. All possible combinations of these variables were tested. Linear discriminant function analysis, using the selected combination of variables, was used to develop a habitat classification model (SAS Institute Inc. 1989:45). The linear combination of variables that maximized the correct classification level with a linear discriminant function analysis was chosen as a final classification model.

We developed a new Habitat Suitability Index (HSI) model for beaver in the Drift Creek Basin using variables that the discriminant function analysis identified as potentially important in distinguishing between dam-sites and unoccupied sites. Using relative frequency distribution of beaver dams over the gradient of each habitat variable (Figure 2), we adjusted values of all the indices to meet characteristics of the stream habitat used by beaver in the basin.

Results

Density and Distribution of Beaver Dams

The stream survey covering 65 km of Drift Creek and its tributaries found 170 beaver dams of which 166 dams (98%) were found in 1st- to 3rd-order streams (map scale 1:24000). Only 4 dams (2%) were found in the 4th-order section, and none were found in 5th-order section of Drift Creek. Average stream widths increased from 1st-order tributaries to the 5th-order main stem of the Drift Creek while average stream gradients decreased (Table 1). Dam

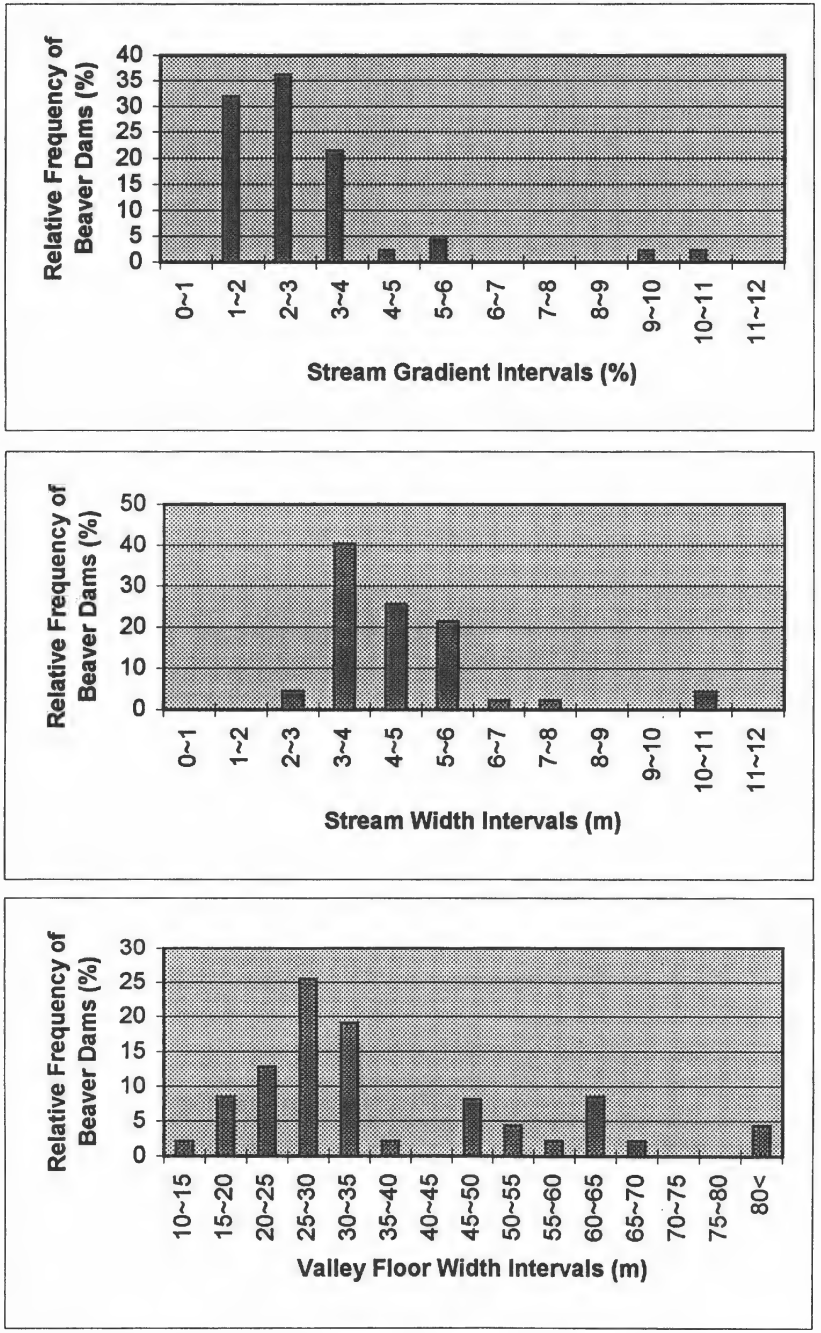


Figure 2. Relative frequency of beaver dams at different stream gradients, stream widths, and valley-floor widths in the Drift Creek Basin, Lincoln County, Oregon, 1988-1989.

density was high in 1st-order and 2nd-order streams and decreased in 3rd-order streams and 4th-order streams (Table 1). The overall dam density was 2.6 dams/km.

TABLE 1. Comparison of mean (SE) stream widths and stream gradients, and beaver dam density among streams with different orders, Drift Creek Basin, Lincoln County, Oregon, 1988-1989.

Stream order[1]	Width (m)	Gradient (%)	Dams/km
1st	3.7(0.1)	3.0(0.3)	4.2
2nd	4.6(0.1)	3.0(0.3)	4.5
3rd	6.2(0.2)	1.3(0.1)	1.5
4th	14.2(0.2)	1.2(0.1)	0.5
5th	26.3(0.3)	0.7(0.1)	0.0

[1]The stream order was determined from the U.S. Geological Survey topographic map (scale 1:24000).

Comparison of Habitat Variables

Percent cover of California hazel, thimbleberry, and huckleberry could not be transformed to attain normal distributions. None of these three variables were different between dam sites and unoccupied-stream sites with Wilcoxon rank-sum tests (Table 2). We were able to test 19 normally-distributed variables with Student's t-tests. Stream gradient and bank slope were lower at dam sites and the valley floor width was wider at dam sites than at unoccupied-stream sites (Table 2). Beaver-dam sites had higher percent cover by forbs and grasses/sedges and had lower percent cover by ferns, shrubs, midstory trees, and total tree canopy than unoccupied-stream sites. Red alder, salmonberry, and stinking currant cover were lower at dam sites than at unoccupied sites. Elderberry cover was higher at dam sites than at unoccupied-stream sites.

Discriminant Analysis

Strong correlations were found between stream width and depth ($r = + 0.60$), valley floor width and bank slope ($r = - 0.70$), shrub cover and salmonberry cover ($r = + 0.70$), and tree-canopy cover and red alder cover ($r = + 0.92$). Correlated variables were tested separately in discriminant analyses. Other variables included in the discriminant analysis were forb cover, fern cover, grass/sedge cover, and Douglas-fir cover.

Three untransformed geomorphic variables (stream width, stream gradient, and valley floor width) and 3 untransformed vegetative variables (total shrub cover, grass/sedge cover, and red alder cover) best separated dam sites from unoccupied sites (Table 3). Increasing valley floor width and grass/sedge cover, and decreasing stream width, stream gradient, red alder cover, and shrub cover were positively associated with dam sites. The model correctly classified 83% of beaver-dam sites and 88% of unoccupied stream sites with the chance-corrected classification rate (Cohen's *Kappa* statistic) of 69% (Titus et al. 1984). The linear discriminant function model was:

$$\begin{aligned} DF = & + 0.069 * (\text{valley floor width [m]}) \\ & - 0.364 * (\text{stream gradient [\%]}) \\ & - 0.545 * (\text{stream width [m]}) \\ & - 0.064 * (\text{red alder cover [\%]}) \\ & - 0.098 * (\text{shrub cover [\%]}) \\ & + 0.024 * (\text{grass/sedge cover [\%]}) \\ & + 9.167. \end{aligned} \quad (1)$$

TABLE 2. Comparison of mean (SE) habitat variables between the beaver-dam sites and unoccupied-stream sites, Drift Creek Basin, Lincoln County, Oregon, 1988-1989.

Variables	Dam sites (n=40)	Unoccupied (n=72)	P-value
Geomorphic			
Stream width (m)	4.1 (0.1)	4.8 (0.2)	0.1192
Stream depth (m)	0.7 (0.1)	0.7 (0.1)	0.2589
Stream gradient (%)	2.2 (0.2)	3.9 (0.4)	0.0007
Valley floor width (m)	32.8 (2.0)	22.7 (1.4)	0.0001
Bank slope (%)	31.8 (2.0)	45.6 (2.8)	0.0015
Vegetative			
Tree canopy (%)	38.8 (2.4)	52.9 (2.3)	0.0001
Overstory tree (%)	22.6 (3.4)	27.8 (2.7)	0.2412
Midstory tree (%)	20.3 (3.1)	29.7 (3.2)	0.0378
Shrub canopy (%)	56.0 (1.6)	65.1 (1.8)	0.0001
Bare ground (%)	9.0 (1.4)	7.6 (1.1)	0.4426
Grass/sedge cover (%)	59.0 (5.0)	25.2 (2.4)	0.0001
Forb Cover (%)	45.0 (2.0)	38.9 (1.7)	0.0280
Fern cover (%)	12.5 (1.7)	18.2 (1.4)	0.0138
Red alder (%)	34.5 (2.9)	47.7 (2.8)	0.0030
Douglas-fir (%)	8.0 (1.8)	8.1 (1.4)	0.9802
Salmonberry (%)	46.5 (2.5)	58.2 (1.8)	0.0003
Elderberry (%)	16.0 (2.3)	10.1 (1.3)	0.0468
Vine maple (%)	13.1 (2.1)	14.3 (1.6)	0.6613
Stinking current (%)	4.9 (2.1)	11.0 (1.5)	0.0039
California hazel (%)	2.0 (0.9)	2.9 (0.9)	0.7465[a]
Thimble berry (%)	7.8 (1.9)	5.2 (1.3)	0.1720[a]
Huckleberry (%)	1.7 (0.7)	0.9 (0.4)	0.1422[a]

[a] P-values of California hazel, thimbleberry, and huckleberry were based on Wilcoxon rank sum tests, and P-values of other variables were based on Student's t-tests.

TABLE 3. Unstandardized and standardized discriminant function coefficients for habitat variables measured at beaver-dam sites and unoccupied sites, Drift Creek Basin, Lincoln County, Oregon, 1988-1989.

Variables	Unstandardized	Standardized	r^1
Valley floor width (m)	+0.069	+0.855	+0.521
Stream gradient (%)	-0.364	-1.001	-0.414
Stream width (m)	-0.545	-0.960	-0.264
Red alder cover (%)	-0.064	-1.419	-0.394
Shrub cover (%)	-0.098	-1.139	-0.502
Grass/sedge cover (%)	+0.024	+0.594	+0.774
Constant	-9.167		

[1]Correlations between habitat variables and a discriminant function axis.

Using DF = 0 as a dividing point, the discriminant function classified positive values (DF>0) as dam sites and negative values (DF<0) as unoccupied sites. Three geomorphic variables, (stream gradient, stream width, and valley floor width) alone correctly classified 83% of dam sites and 67% of unoccupied sites with the chance-corrected classification rate (*Kappa* statistic) of 50%. The linear discriminant function model of geomorphic variables was:

$$DF = -0.484 * (\text{stream width [m]}) + 0.060 * (\text{valley floor width [m]}) - 0.239 * (\text{stream gradient [\%]}) + 1.210. \quad (2)$$

Developing a New Habitat Suitability Index (HSI) Model

We developed a new HSI model using the habitat data collected from the Drift Creek Basin. Three geomorphic attributes, which were selected in the discriminant analysis, were used to construct the following indices: stream gradient index, stream width index, and valley floor width index. Each index produces index scores (IS) for a particular attribute ranging from IS = 0.0 for unsuitable to IS = 1.0 for optimum condition for dam sites (Figure 3). An index score of each attribute is interpolated from the index diagram for a value of that attribute measured at a given site (Figure 3). Scores for the 3 indices are obtained for a site and compared to determine an HSI score, which represents a measure of overall habitat suitability of a site for dam building. In this HSI model, the minimum score among the 3 index scores is selected as an HSI score of a given site.

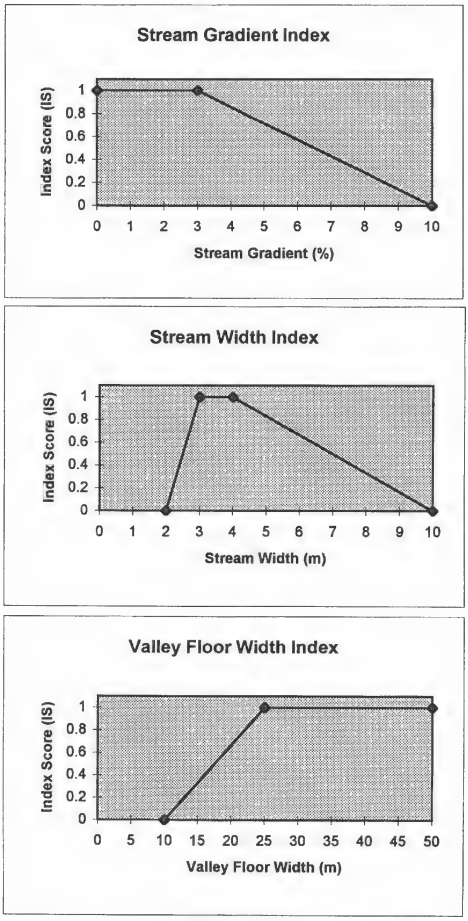


Figure 3. Diagrams of index scores for stream gradient, stream width, and valley-floor-width index in the new HSI model for beaver based on the data from the Drift Creek Basin, Lincoln County Oregon, 1988-1989.

Stream Gradient Index

In the Drift Creek Basin 67% of beaver dams were found on the streams that had gradient < 3% (Figure 2). Frequency of dams decreased as stream gradient increased from 3% to 10%. No beaver dams were observed on streams with a gradient > 10%. Therefore, stream gradients < 3% were considered optimum (IS = 1.0) for dam sites, stream

gradients > 10% were considered unsuitable (IS = 0.0), and the suitability of stream gradient was assumed to decline linearly from gradient 3% to 10% (Figure 3).

Stream Width Index

We found beaver dams most frequently on the streams 3 - 4 m wide (Figure 2). Dam frequency decreased as the streams became wider. No beaver dams were found in the streams that had widths > 10 m or < 2 m. Therefore, streams 3 - 4 m wide were considered optimum for dam sites (IS = 1.0, Figure 3), while stream widths < 2 m or > 10 m were considered unsuitable for dam sites (IS = 0.0). Suitability of stream width was assumed to decline linearly from 3 m to 2 m and also from 4 m to 10 m.

Valley Floor Width Index

In the Drift Creek Basin, beaver dams were most frequently found on streams that had valley floors 25 - 30 m wide (Figure 2). Seventy-seven percent of dams were found on streams that had valley floors > 25 m wide. In the U.S. Fish and Wildlife HSI model, streams that had valley floors > 46 m wide were considered optimum as dam sites (Allen 1983). Although such wide valley floors were rare in the 1st- to 3rd-order mountain streams of the Drift Creek Basin, we found beaver dams on almost all the stream survey sites with valley floor widths > 50 m. No beaver dams were found on the streams that had valley floors < 10 m wide. Therefore, valley floor widths > 25 m were considered optimum for beaver dam sites (IS = 1.0, Figure 3) and valley floor widths < 10 m were considered unsuitable for dam sites (IS = 0.0). Suitability of the valley floor width was assumed to decline linearly from 25 m to 10 m.

HSI scores

To determine an HSI score for a given site, index scores (IS) for stream gradient, stream width, and valley floor width are obtained from the index diagrams (Figure 3). We assume stream gradient, stream width, and valley floor width cannot substitute for one another to improve overall habitat quality. Among these three attributes, we assume that the one with the least favorable condition for dam building, indicated by the lowest index score, is limiting the overall habitat suitability of the site. For example, beaver cannot build dams in very wide streams (>10 m) even though stream gradients are at optimum conditions (<3%). In these cases, the unfavorable stream width is limiting the overall habitat suitability of dam sites (Table 1). Based on the concept that one factor can limit habitat suitability (U.S. Fish and Wildlife Service 1981:103-ESM-3-31), the model uses the lowest index score (IS) of either stream gradient index, stream width index, or valley floor width index as the HSI score of the site, which represents the measure of overall habitat suitability of the site for dam building. For example, a hypothetical stream section with a gradient of 3%, a stream width of 6 m, and a valley floor width of 15 m would have IS = 1.0 for gradient index, IS = 0.7 for stream width index, IS = 0.3 for valley floor width index, and HSI score = 0.3 (Figure 3). In this scenario, the model considers valley floor width as limiting the overall habitat suitability of the site.

Discussion

Vegetative and Physical Characteristics of Beaver Dam Sites

Decreasing red alder cover and shrub cover, and increasing grass/sedge cover were positively associated with dam sites in the first discriminant function model (equation 1, Table 3). If the observed differences in vegetative variables between dam sites and unoccupied sites were the result of alteration by beaver, the vegetative variables would not be good predictors of potentially suitable sites prior to the colonization by beaver (Beier and Barrett 1987). Beaver can alter species composition of riparian plant communities by removing preferred species and stimulating the growth of avoided species (Barnes and Dibble 1988, Johnston and Naiman 1990). In the Oregon Coast Range beaver selectively forage on red alder and salmonberry and avoid foraging on elderberry (Bruner 1990). Thus, the selective foraging by beaver probably reduced the red alder and salmonberry cover and indirectly increased the elderberry cover at the dam sites. Abundance of herbaceous vegetation at the dam sites was probably a result of removal of tree and shrub cover and increased soil moisture around the beaver pond (Beier and Barrett 1987). Consequently, the discriminant model, when vegetative variables were included, would not likely identify potential dam sites in streams of the Oregon Coast Range.

Physical characteristics of stream habitats have been found to be more important factors of dam-site selection than vegetative characteristics (Howard and Larson 1985, Beier and Barrett 1987). We found that decreasing gradients and stream widths and increasing valley floor widths were positively associated with dam sites. Beier and Barrett (1987) and Howard and Larson (1985) also indicated that decreasing gradients were positively correlated with dam occurrence, but that decreasing stream widths were negatively correlated with dam site presence.

Frequency of beaver dams in the Drift Creek basin decreased as streams became steeper or wider (Figure 2). The force created by stream flow is probably too large for beaver to build and maintain dams on high-gradient streams (>10%) or on wide streams (>10 m) with deep channels that carry large volume of water per unit length (McComb et al. 1990). Taylor (1970:142) indicated that flood damage to beaver dams was most evident on slightly steep and undivided stream channels. Bruner (1990) reported that nearly all beaver dams in 4th- and 5th-order coastal streams of Oregon were washed out annually.

Valley floor width was also important to dam-site location in the basin. Beaver dams that flood a wide valley floor create ponds with large surface area and long perimeter relative to volume (Johnston and Naiman 1987). During a flood, water tables may rise only a few cm; a series of such ponds effectively store water and reduce peak discharge (Parker et al. 1985). Beaver dams can also significantly reduce velocity of increased discharge by spreading stream flow over a wider valley floor (Parker et al. 1985). In contrast, beaver ponds constructed on a high-gradient stream with a narrow valley floor tend to be small in surface area and perimeter relative to volume (Johnston and Naiman 1987). During a flood, the water level of such ponds can increase drastically; therefore, the ponds are not effective at reducing peak discharge and flow velocity. Consequently, beaver dams in narrow valleys are probably more susceptible to being washed out during floods than those in wide valleys.

Classification Models and Management Implications

Based on the 3 geomorphic variables (stream width, stream gradient, valley floor width), the new HSI model can be used to evaluate suitability of stream sites as dam sites. Alternatively, the discriminant function model with the same geomorphic variables (equation 2) can be used to classify stream sites as either dam sites or unoccupied sites.

The HSI model and the discriminant function model can be best applied for streams of the Drift Creek Basin and should be applicable for other streams of the Oregon Coast Range as long as geomorphology and hydrology are similar to those of the Drift Creek Basin. We recommend that our models be tested in watersheds in different geographic locations with various environmental conditions to ensure a wider geographic scope of applicability.

Our habitat models cannot predict local beaver populations or habitat suitability for bank-dwelling beavers; however, wildlife managers can use these models to inventory potential beaver-dam sites along streams of the Oregon Coast Range. Information obtained from our models can be incorporated into plans to preserve riparian habitats because beaver dams and associated beaver activities influence various ecological attributes and processes, including abundance and community structures of aquatic and terrestrial organisms (Rutherford 1955, Reese and Hair 1976, McDowell and Naiman 1986, Bruner 1990), vegetation dynamics (Barnes and Dibble 1988, Johnston and Naiman 1990), biochemical pathways (Naiman et al. 1986, Naiman et al. 1988), and sediment transport (Parker et al. 1985). Ultimately, these new habitat classification models will help land managers consider how to minimize the adverse influence of land use practices on unique riparian habitats maintained by beaver.

Acknowledgements

We thank J. S. Schwartz for providing us with additional field information, and S. W. Overton and J. R. Sedell for comments on an early draft of the manuscript. We also thank T. Sabin for advice with statistical analyses. K. A. Avina, E. Helmer, and R. Hess reviewed early drafts of this manuscript. Funding for this project was provided through the Coastal Oregon Productivity Enhancement (COPE) program. COPE is a cooperative research and technology transfer effort among Oregon State University, USDA Forest Service, USDI Bureau of Land Management, other state and federal agencies, industry, county governments. and resource associations.

Literature Cited

Allen, A. W. 1983. Habitat suitability index models: beaver. U.S. Dep. Inter., Fish and Wildl. Serv. FWS/OBS-82/10.30 Revised. 20p.

Anderson, S. 1964. Return of the beaver. Nat. Hist. 73:38-43.

Apple, L. L. 1985. Riparian habitat restoration and beavers. *In* R. R. Johnson et al. (Tech. Coords) Riparian ecosystems and their management: reconciling conflicting uses. Proc. First North American Riparian Conference. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. RM-120. Pp. 489-49.

Barnes, W. J., and E. Dibble. 1988. The effects of beaver in riverbank forest succession. Can. J. Bot. 66:40-44.

Beier, P., and R. H. Barrett. 1987. Beaver habitat use and impact in Truckee River Basin, California. J. Wildl. Manage. 51:794-799.

Bruner, K. L. 1990. Effects of beaver on streams, streamside habitat, and coho salmon fry populations in two coastal Oregon streams. Oregon State University, Corvallis. M.S. Thesis.

Brayton, D. S. 1984. The beaver and the stream. J. Soil Water Conserv. 39:18-109.

Devore, J. L., and R. L. Peck. 1986. Statistics, the exploration and analysis of data. West Publishing Company, St. Paul, Minnesota.

Guthrie, D., and J. Sedell. 1988. Primeval beaver stumped Oregon Coast trappers. News & Views, Department f Fisheries and Wildlife, Oregon State University June:14-16.

Howard, R. J., and J. S. Larson. 1985. A stream habitat classification system for beaver. J. Wildl. Manage. 49:19-25.

Johnston, C. A., and R. J. Naiman. 1987. Boundary dynamics at the aquatic-terrestrial interface: The influence of beaver and geomorphology. Landscape Ecol. 1:47-57.

_____. 1990. Browse selection by beaver: effects on riparian forest composition. Can. J. For. Res. 20:1036-1043.

McComb, W. C., J. R. Sedell, and T. D. Buchholz. 1990. Dam-site selection by beavers in an eastern Oregon basin. Great Basin Naturalist 50:273-383.

McDowell, D. M., and R. J. Naiman. 1986. Structure and function of a benthic invertebrate stream community as influenced by beaver (*Castor canadensis*). Oecologia 68:481-489.

Naiman, R. J., C. A. Johnston, and J. C. Kelley. 1988. Alteration of North American streams by beaver. BioScience 38:753-762.

Naiman, R. J., J. M. Meillo, and J. E. Hobbie. 1986. Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). Ecology 67:1254-1269.

Parker, M., F. J. Wood, Jr., B. H. Smith, and R. G. Elder. 1985. Erosional downcutting in lower order riparian ecosystems: Have historical changes been caused by removal of beaver? *In* R. R. Johnson et al. (Tech. Coords) Riparian ecosystems and their management: reconciling conflicting uses. Proc. First North American Riparian Conference. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. RM-120. Pp. 35-38.

Reese, K. P., and J. D. Hair. 1976. Avian species diversity in relation to beaver pond habitats in the Piedmont region of South Carolina. Proc. Annu. Conf. Southeast. Assoc. Game and Fish Comm. 13:437-447.

Rutherford, W. H. 1955. Wildlife and environmental relationships of beavers in Colorado forests. J. For. 53:803-806.

SAS institute, INC. 1989. SAS/STAT user's guide, version 6, fourth edition. SAS Institute Inc., Cary, North Carolina.

_____. 1990. SAS Procedures guide, version 6, third edition. SAS Institute Inc., Cary, North Carolina.

Schwartz, J. S. 1991. Influence of geomorphology and land use on distribution and abundance of salmonids in a Coastal Oregon Basin. Oregon State University, Corvallis. M.S. Thesis.

Sedell, J. R., and J. L. Froggatt. 1984. Importance of streamside forests to large rivers: isolation of the Willamette River, Oregon, U.S.A. from its floodplain by snagging and stream forest removal, Verh. Internat. Verin. Theor. Ange. Limnol. 22:1828-34.

Seton, J. R. 1929. Lives of game animals. Vol.4, Part 2, Rodents, etc. Doubleday, Doran, Garden City, New York.

Slough, B. G., and R. M. S. Sadleir. 1977. A land capability classification system for beaver (*Castor canadensis* Kuhl). Can. J. Zool. 55:1324-1335.

Suzuki, N. 1992. Habitat classification and characteristics of small mammal and amphibian communities in beaver-pond habitats of the Oregon Coast Range. Oregon State University, Corvallis. M.S. Thesis.

Taylor, D. 1970. Growth, decline, and equilibrium in a beaver population at Sagehen Creek, California. University of California, Berkeley. Ph.D. Dissertation.

Titus, K., J. A. Mosher, and B. K. Williams. 1984. Chance-corrected classification for use in discriminant analysis: Ecological applications. The Am. Midl. Natur. 111:1-7.

U.S. Fish and Wildlife Service. 1981. Standards for the development of habitat suitability index models. ESM-103. U.S. Dep. Inter., Fish and Wildl. Serv., Div. Ecol. Serv. Washington, D.C.

Received 25 August 1997
Accepted for publication 26 January 1998

Albert G. Wilson, Jr., Department of Life Sciences, Spokane Falls Community College, MS 3180, 3410 Fort George Wright Drive, Spokane, Washington 99224-5288

John H. Larsen, Jr., Department of Zoology, Washington State University, Pullman, Washington 99164-4210

Biogeographic Analysis of the Coeur d'Alene Salamander *(Plethodon idahoensis)*

Abstract

We constructed a map comparing the U.S. geographic range of the Coeur d'Alene salamander (*Plethodon idahoensis*) with climatic and geological variables. Lilac bloom dates were used to approximate 1,100-1,800 m upper altitudinal limits for the salamander. *Plethodon idahoensis* occupies temperate regions of the northern Rocky Mountains with at least 50 cm average annual precipitation, and appears to be geographically restricted by unconsolidated geological deposits. Our map identifies regions potentially inhabited by *P. idahoensis*, and may therefore be useful in future study and protection of this species.

Introduction

The Coeur d'Alene salamander (*Plethodon idahoensis*) is a terrestrial amphibian inhabiting northern Idaho, northwestern Montana, and southeastern British Columbia; it is the sole lungless salamander (Plethodontidae) of the northern Rocky Mountains (Nussbaum et al. 1983, Holmberg et al. 1984). Although the species' geographic range has been largely defined (Orchard 1991, Wilson et al. 1997), much of the area inhabited by *P. idahoensis* remains unsurveyed. Little is known of specific factors that influence the salamander's occurrence, and potential habitat has not been identified.

We used cartographic methods (Lynch 1981) to compare the distribution of *P. idahoensis* with variables known to influence occurrence of other terrestrial salamanders. These include levels of precipitation and annual duration of cold weather, which affect foraging (Lynch 1981) and reproduction (Houck 1977), and the presence of rocky microhabitat, which can affect availability of shelter and nesting sites (Bury et al. 1991). Our objective was to produce a map that identifies limiting factors and reveals regions potentially inhabited by *P. idahoensis*.

Methods

We compiled localities from museum and field surveys of Wilson et al. (1997). These are listed with the Idaho Natural Heritage Program, Boise, and the Montana Natural Heritage Program, Helena. Localities were plotted on U.S. Geological Survey topographic maps (1:500,000 scale) to provide a base for environmental factors. We transferred the isohyet of lowest value encompassing all populations from average annual precipitation maps (USDA Soil Conservation Service 1965a, 1965b, 1965c; Pacific Northwest River Basins Commission 1969) to outline regions having at least the minimum average precipitation in which the salamander occurs.

Because annual temperature variation has not been directly measured and mapped in the northern Rockies, we used the average first bloom date of the common purple lilac (*Syringa vulgaris*) to index regionally the duration of cold weather (Caprio 1966, 1970). Locality elevations were obtained from U.S. Geological Survey topographic maps (1:24,000 scale). To reveal how cold may affect the salamander's distribution we examined bloom dates for high-elevation localities, and assumed the latest date among all localities represented an annual temperature regime near a lower tolerance limit for the species. To our base map, we then transferred published isophenes depicting geographic variation of this bloom date relative to elevation (Caprio 1966). We used these isophenes to draw topographic contours on the base map denoting variation in the altitudinal limits of the salamander.

Regions underlain by unconsolidated Quaternary deposits (aeolian, alluvial, glacial, and lacustrine) were transferred to our base map from geologic maps (Ross et al. 1958, Huntting et al. 1961,

© 1998 by the Northwest Scientific Association. All rights reserved.

Bond and Wood 1978, Walker and Macleod 1991). These represent areas in which rock outcrops and rocky colluvium are rare. A final map showing localities, climatic regions, and unconsolidated deposits was produced with NIH Image 144b and Deneba CANVAS 3.0 computer programs.

Results

The minimum average annual precipitation associated with *P. idahoensis* is 50 cm for a locality on the Clark Fork River, Montana (47°, 23', 23" N; 115°, 48', 32" W; 760 m elev.). The Columbia Plateau and drainages of the Salmon, Bitterroot, and Flathead Rivers receive less than this amount and circumscribe the salamander's U.S. distribution (Figure 1). Except along the southern extent of the species' occurrence these lowlands are also underlain by unconsolidated Quaternary deposits. Unconsolidated deposits flanking the Selkirk Mountains are within the climatic range of the salamander and bound the northwestern limit of its U.S. distribution.

The latest average annual *S. vulgaris* bloom date for any locality is 14 June for a site in the Kootenai River drainage, Montana (48°, 39', 36" N; 115°, 39' W; 1,300 m elev.). This date projected to other sections of the region predicts an upper altitudinal limit for *P. idahoensis* that varies from 1,100 m on the northwest tip of the Idaho Panhandle to 1,800 m at the southern end of the species' geographic range. Regions above these presumptive limits are prominent at the northern, eastern, and southern margins of the salamander's distribution; and form the crest of the Bitterroot Range, which separates Montana populations from those in Idaho.

In Montana, *P. idahoensis* occupies narrow corridors of suitable climate in the Kootenai and Clark Fork River drainages. On the west slope of the Bitterroot Range of Idaho, the salamander occurs only sparsely across a continuous region of favorable conditions. Most Idaho localities occur upslope in canyons draining the Bitterroots.

Discussion

Climatic regions suitable for *P. idahoensis* encompass the disjunct coastal forest province of the northern Rockies (Heusser 1983, Cooper et al. 1991). The salamander is associated with this province, except for its apparent absence from the Selkirk Mountains. Projected upper altitudinal limits of *P. idahoensis* correspond with the transition from temperate to subalpine communities (Krajina 1969, Arno 1979, Habeck 1987). The Bitterroot Range, with its comparatively low elevations and strong maritime climate (Cooper et al. 1991), contains most potential habitat for the species.

Plethodon idahoensis localities are most abundant in Bitterroot uplands where near-coastal (75-140 cm) annual precipitation levels exist (USDA Soil Conservation Service 1965a). These uplands also support the region's greatest diversity of coastal disjunct plants, invertebrates and amphibians (Nussbaum et al. 1983, Johnson 1987, Lorain 1988). Populations of *P. idahoensis* in xeric surrounding areas occupy favorably moist microhabit (Wilson et al. 1997).

The lack of populations in climatically suitable areas of the Selkirk lowlands indicates that unconsolidated deposits limit distribution of *P. idahoensis*. Such deposits likely influenced the salamander's current geographic range by limiting post-Pleistocene dispersal (Lynch 1984). The absence of *P. idahoensis* from mountains east of the Bitterroot Range, for example, is correlated with widespread occurrence of glacio-alluvial barriers in intervening valleys. Although alluvial deposits restrict dispersal by *Plethodon*, rocky uplands paralleling a river can provide dispersal corridors (Thurow 1968). Both the Kootenai and Clark Fork Rivers trend northward and thus helped effect the latitudinal breadth of the salamander's present distribution. All known Canadian populations are in the Kootenai drainage (Orchard 1991).

Syringa vulgaris phenological data are not available for Canada, so we did not include Canadian lands in our analysis. However, if isophenes published for the U.S. (Caprio 1966) are projected onto Canadian topographic maps, an upper altitudinal limit for *P. idahoensis* of 750 m is indicated for the northern end of the Kootenai Valley, 200 km north of the U.S.-Canadian border. This valley receives sufficient precipitation for *P. idahoensis* along its entire length (Farley 1979) and is worthy of more surveys.

Plethodon idahoensis is most closely related to Van Dyke's salamander (*Plethodon vandykei*) of western Washington. There has even been debate as to whether the two forms actually comprise a single species (Howard et al. 1993). Although *P. idahoensis* occupies drier habitats, both species

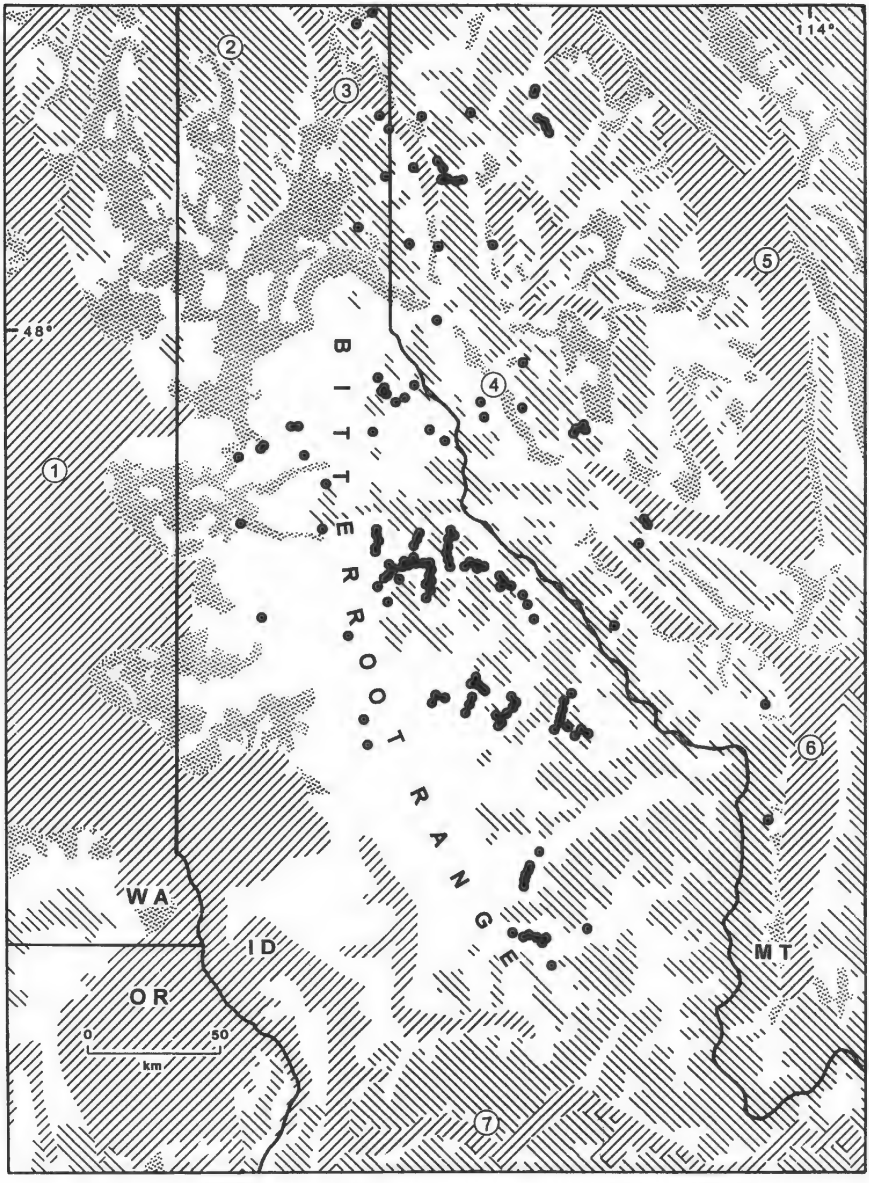


Figure 1. The U.S. distribution of *Plethodon idahoensis* relative to three environmental factors. Closed circles represent localities. Regions with less than 50 cm average annual precipitation are represented by hatching directed upward to the right. Hatching directed upward to the left delimits regions with average *Syringa vulgaris* bloom dates later than 14 June. Stippling indicates unconsolidated Quaternary deposits. For visual clarity, unconsolidated deposits are depicted only within the climatic range of the salamander, and the following geographic features are represented by numbers: Columbia Plateau (1), Selkirk Mountains (2), Kootenai River (3), Clark Fork River (4), Flathead Valley (5), Bitterroot Valley (6), Salmon River (7).

inhabit temperate mesophytic forests and have similar upper altitudinal limits (Wilson et al. 1995). Paleobotanical evidence (Detling 1968, Daubenmire 1975) and molecular estimates of the timing of speciation in Pacific Northwest amphibians (Highton and Larson 1979, Daugherty et al. 1983) suggest that vicariance of *P. idahoensis* and *P. vandykei* originated during a pre-Pleistocene xerification of the Columbia Plateau. This event, which resulted from development of the Cascade Mountains rainshadow (Smiley 1963), also helped to isolate other elements of the Rocky Mountain disjunct coastal biota (Daubenmire 1975, Johnson 1987).

Speculations of more recent occurrence of *P. idahoensis* or *P. vandykei* on the Columbia Plateau or in uplands to the north (Savage 1952, Wake 1966, Howard et al. 1993) are not supported by our analysis. These regions are largely outside of the geological and climatic ranges that presently favor occurrence by either species (Pacific Northwest River Basins Commission 1969, Farley 1979, Wilson et al. 1995) and were dominated by sagebrush steppe with subalpine arboreal elements during Pleistocene glacial maxima (Barnosky et al. 1987).

Our study suggests that *P. idahoensis* is restricted to Rocky Mountain regions north of the Salmon River. Isolated populations may yet be encountered in the Bitterroot Range and in mountainous regions west of the Flathead Valley of Montana. Much of the southern Bitterroots is inaccessible by road and has been inadequately searched. By identifying potential habitat in these and other areas we hope to facilitate future surveys and thus enable protection and further study of this unique species.

Acknowledgements

We received support from the Natural Heritage Programs of Idaho and Montana, USDA Forest Service, USDI Bureau of Land Management, and Washington State Department of Wildlife. We are grateful for advice from Joseph Caprio, Myron Malnau, and Donald Satterlund; and for technical assistance from Daniel Bivens, Chris Davitt, and Joan Follwell. The manuscript was improved by comments from Keith Aubrey, Richard Johnson, Don Miller, Richard Wallace, and one anonymous reviewer.

Literature Cited

Arno, S.F. 1979. Forest regions of Montana. USDA For. Serv. Res. Pap. INT-218. Interm. For. Range Exp. Sta., Ogden, UT. 39 p.

Barnosky, C.W., P.M. Anderson, and P.J. Bartlein. 1987. The northwestern U.S. during deglaciation; vegetational history and paleoclimatic implications. *In* W.F. Ruddiman and H.E. Wright, Jr. (eds.), North America and adjacent oceans during the last deglaciation. Geol. Soc. No. Am. Boulder, CO. Pp. 289-321.

Bond, J.G., and C.H. Wood. 1978. Geologic map of Idaho. Idaho Dept. Lands, Bureau Mines and Geol., Moscow.

Bury, R.B., Corn, P.S., and K.B. Aubry. 1991. Regional patterns of terrestrial amphibian communities in Oregon and Washington. *In* L.F. Ruggiero, K.B. Aubry, A.B. Carey, and M. H. Huff (eds.), Wildlife and vegetation of unmanaged Douglas-fir forests. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-285. Pac. Northw. Res. Sta., Portland, OR. Pp. 341-350.

Caprio, J.M. 1966. Pattern of plant development in the western United States. Mont. Agr. Exp. Sta. Bull. 607:1-42.

_____. 1970. Areal and temporal variations in developmental phases of *Syringa vulgaris* L. throughout the western United States. Utah State University, Logan. Ph.D. Dissertation.

Cooper, S.V., K.E. Neiman, R. Steele, and D.W. Roberts. 1991. Forest habitat types of northern Idaho: a second approximation. USDA For. Ser. Gen. Tech. Rep. INT-236. Interm. For. Range Exp. Sta., Ogden, UT. 143 p.

Daubenmire, R. 1975. Floristic plant geography of eastern Washington and northern Idaho. J. Biogeog. 2:1-18.

Daugherty, C.H., F.W. Allendorf, W.W. Dunlap, and K.L. Knudsen. 1983. Systematic implications of geographic patterns of variation in the genus *Dicamptodon*. Copeia 1983:679-691.

Detling, L.E. 1968. Historical background of the flora of the Pacific Northwest. Univ. Or. Mus. Nat. Hist. Bull. 13:1-57.

Farley, A.L. 1979. Atlas of British Columbia. University of British Columbia Press, Vancouver, BC.

Habeck, J.R. 1987. Present-day vegetation in the northern Rocky Mountains. Ann. Missouri Bot. Garden 74:804-840.

Heusser, C.J. 1983. Vegetational history of the Northwest including Alaska. *In* S.C. Porter (ed.), Late-Quaternary environments of the United States, Vol. 1. University of Minnesota Press, Minneapolis. Pp. 239-258.

Highton, R., and A. Larson. 1979. The genetic relationships of the salamanders of the genus *Plethodon*. Sys. Zool. 28:579-599.

Holmberg, R.G., N.P.D. Angerilli, and L.J. LaCasse. 1984. Overwintering aggregations of *Leiobunum paessleri* in caves and mines (Arachnida, Opiliones). J. Arachnol. 12:195-205.

Houck, L.D. 1977. Life history patterns and reproductive biology of neotropical salamanders. *In* D.H. Taylor and S.I. Guttman (eds.), The reproductive biology of amphibians. Plenum Publishing Corp., Chicago, IL. Pp. 43-72.

Howard, J.H., L.W. Seeb, and R.L. Wallace. 1993. Genetic variation and population divergence in the *Plethodon vandykei* species group. Herpetologica 49:238-247.

Huntting, M.T., W.A.G. Bennet, V.E. Livingston, Jr., and W.S. Moen. 1961. Geologic map of Washington. Wash. Dept. Conserv., Div. Mines and Geol., Olympia.

Johnson, P.J. 1987. Larval taxonomy, biology, and biogeography of the genera of North American Byrrhidae (Insecta: Coleoptera). University of Idaho, Moscow. M.S. Thesis.

Krajina, V.J. 1969. Ecology of forest trees in British Columbia. *In* V.J. Krajina and R.C. Brooke (eds.), Ecology of western North America, Vol. 2. Dept. of Bot., Univ. British Columbia, BC, Canada. Pp. 1-146.

Lorain, C.C. 1988. Floristic history and distribution of coastal disjunct plants of the northern Rocky Mountains. University of Idaho, Moscow. M.S. Thesis.

Lynch, J.E., Jr. 1984. Reproductive ecology of *Plethodon idahoensis*. University of Idaho, Moscow. M.S. Thesis.

Lynch, J.F. 1981. Patterns of ontogenetic and geographic variation in the black salamander, *Aneides flavipunctatus* (Caudata: Plethodontidae). Smithson. Contrib. Zool. 324:1-53.

Nussbaum, R.A., E.D. Brodie, Jr., and R.M. Storm. 1983. Amphibians and reptiles of the Pacific Northwest. University of Idaho Press, Moscow.

Received 7 January 1998
Accepted for publication 17 March 1998

Orchard, S.A. 1991. Amphibian population declines in British Columbia. *In* C.A. Bishop and K.E. Pettit (eds.), Declines in Canadian amphibian populations: designing a national monitoring strategy. Can. Wildl. Serv. Occ. Pap. 76. Can. Wildl. Serv., Ottawa, Ontario. Pp. 10-13.

Pacific Northwest River Basins Commission. 1969. Climatological handbook, Columbia Basin states precipitation, vol. 2. Env. Sci. Serv. Admin., Washington, DC.

Ross, C.P., D.A. Andrews, and I.J. Witkind. 1958. Geologic map of Montana. Mont. Bureau Mines and Geol., Helena, MT.

Savage, J.M. 1952. The distribution of the Pacific giant salamander, *Dicamptodon ensatus*, east of the Cascade Mountains. Copeia 1952:183.

Smiley, C.J. 1963. The Ellensburg flora of Washington. Univ. Calif. Publ. Geol. Sci. 35:159-276.

Thurow, G.R. 1968. On the small black *Plethodon* problem. West. Ill. Univ. Ser. Biol. Sci. 6:1-48.

USDA Soil Conservation Service. 1965a. Map of mean annual precipitation, State of Idaho. U.S. Weather Bureau Riv. Forecast Center, Portland, OR.

_____. 1965b. Map of mean annual precipitation, State of Oregon. U.S. Weather Bureau Riv. Forecast Center, Portland, OR.

_____. 1965c. Map of mean annual precipitation, State of Washington. U.S. Weather Bureau Riv. Forecast Center, Portland, OR.

Wake, D.B. 1966. Comparative osteology and evolution of the lungless salamanders, family Plethodontidae. Mem. So. Calif. Acad. Sci. 4:1-111.

Walker, G.W., and N.S. Macleod. 1991. Geologic map of Oregon. USDI, U.S. Geol. Survey Publ., Washington, DC.

Wilson, A.G., Jr., J.H. Larsen, Jr., and K.R. McAllister. 1995. Distribution of Van Dyke's Salamander (*Plethodon vandykei* Van Denburgh). Am. Midl. Nat. 134:388-393.

Wilson, A.G., E.M. Wilson, C.R. Groves, and R.L. Wallace. 1997. Distribution of the Coeur d'Alene Salamander (*Plethodon idahoensis* Slater and Slipp). Gr. Basin Nat. 57:359-362.

George T. McCabe, Jr., Susan A. Hinton, and **Robert L. Emmett**
Fish Ecology Division, Northwest Fisheries Science Center, National Marine Fisheries Service,
National Oceanic and Atmospheric Administration, 2725 Montlake Boulevard East, Seattle, Washington 98112-2097

Benthic Invertebrates and Sediment Characteristics in a Shallow Navigation Channel of the Lower Columbia River, Before and After Dredging

Abstract

Little is known about the impact of dredging on benthic invertebrates in navigation channels of the lower Columbia River. To help fill this informational void, we conducted benthic invertebrate and sediment studies in a shallow navigation channel in the river before and after dredging. Benthic invertebrate and sediment samples were collected with a 0.1-m^2 Van Veen grab sampler at seven stations in the Wahkiakum County Ferry Channel, Washington (River Kilometer 70), and at an upstream reference area in 1993-1995. No significant effects ($P > 0.05$) of the ferry channel dredging project on *Corbicula fluminea*, Ceratopogonidae larvae, *Corophium* spp., or total benthic invertebrate densities were detected in the statistical analysis, although benthic invertebrate densities were significantly different ($P < 0.05$) between surveys and areas for some organisms. During all eight surveys, *Corbicula fluminea*, *Corophium* spp., and Ceratopogonidae (Diptera) larvae were generally the most common benthic invertebrates in both the ferry channel and the reference area. Two measures of community structure, Diversity (H) and Equitability (E), were calculated for each area for each survey. No significant effects ($P > 0.05$) of the ferry channel dredging project on the benthic invertebrate community structure, as measured by H and E, were detected. No significant effects ($P > 0.05$) of the ferry channel dredging project on sediment median grain size or percent volatile solids were detected. Results from this study will provide information to aquatic resource agencies that assess the potential environmental effects of dredging in similar habitats of the lower Columbia River.

Introduction

The lower Columbia River from the mouth to Portland, Oregon, is an important navigation channel that is maintained to a depth of 12.2 m by dredging. In addition, various shallower, secondary navigation channels in the lower river are maintained through dredging. Little is known about the impact of dredging on benthic invertebrates in the lower Columbia River. To help fill this informational void, we conducted benthic invertebrate and sediment studies in the Wahkiakum County Ferry Channel, Washington (River Kilometer (RKm) 70), before and after dredging of the channel.

The Wahkiakum County Ferry, which is owned and operated by Wahkiakum County and subsidized by the State of Washington, operates between Westport, Oregon, and Puget Island, Washington. Prior to our surveys, shoaling in the ferry channel between Puget Island and the main navigation channel of the Columbia River forced the ferry to operate at one-half capacity during part of the year (U.S. Army Corps of Engineers 1992). Clamshell dredging was conducted in about 244 m of the ferry channel from 24 January to 17 February 1994. About 14,258 m^3 of sediments were removed from the channel and disposed of at an in-water disposal site about 4 km downstream from the ferry channel. Although the ferry channel is about 579 m long, only about 244 m had to be dredged, as the remainder of the channel is naturally deep. The dredged portion of the ferry channel is 61 m wide and authorized to a depth of 2.7 m.

Although the area of the dredging project was small, there was concern that benthic invertebrates, particularly the amphipods *Corophium* spp. (*C. salmonis* and *C. spinicorne*), would be adversely impacted. *Corophium* spp. are frequently found in intertidal and shallow subtidal habitats of the Columbia River estuary and are seasonally important in the diets of juvenile salmonids and other fishes (McCabe et al. 1983, 1986; Kirn et al. 1986; Muir et al. 1988). *Corophium salmonis* and *C. spinicorne* were the dominant prey for juvenile salmonids collected during the spring of 1984 at Bonneville Dam, the lowermost dam on the Columbia River (Muir and Emmett 1988).

© 1998 by the Northwest Scientific Association. All rights reserved.

The goals of the present study were 1) to describe benthic invertebrate communities in the dredged portion of the ferry channel before and after dredging and 2) to assess recolonization by benthic invertebrates in the dredged portion of the ferry channel. We collected samples in a reference area located about 3.2 km upstream from the ferry channel to help assess the effects of dredging. Specifically, we assessed benthic invertebrate species composition, standing crops, diversity, and equitability in both the ferry channel and the upstream reference area. Results from this study will provide information to aquatic resource agencies that assess the potential environmental effects of dredging in similar habitats of the lower Columbia River.

Methods

Sampling

Benthic invertebrate and sediment samples were collected at seven stations each in the Wahkiakum County Ferry Channel and an upstream reference area in October 1993; January, February, April, July, and October 1994; and January and April 1995 (Figure 1). Sampling in October 1993 and January 1994 was conducted prior to dredging in the ferry channel, and sampling in February 1994 was conducted 6 days after dredging was completed. Mean water depths, by survey, in the ferry channel and reference area ranged from 2.0 to 3.8 m and 2.3 to 4.7 m (mean lower low water), respectively. Sampling stations were located using a radar range-finder and the Global Positioning System (GPS).

At each of the 14 stations, a 0.1-m^2 Van Veen grab sampler was used to collect four samples; three were analyzed for benthic invertebrates and one for sediment type. Each benthic invertebrate sample was initially preserved in a buffered formaldehyde solution (≥4%) containing rose bengal, an organic stain. Later each benthic invertebrate sample was washed with water through a 0.5-mm screen. All benthic invertebrates were sorted from each sample, identified to the lowest practical taxon, counted, and stored in 70% ethanol. The sediment sample from each station was placed in a labeled plastic bag, refrigerated, and analyzed for grain size, percent silt/clay, and percent volatile solids by the U.S. Army Corps of Engineers, North Pacific Division Materials Laboratory, Troutdale, Oregon.

Data Analyses

Benthic invertebrate data were analyzed by station to determine species composition, densities (by taxon and total), and community structure (diversity and equitability). The Shannon-Wiener function (H) was used to determine diversity (Krebs 1978), which was expressed as:

$$H = -\sum_{i=1}^{s} (p_i)(\log_2 p_i)$$

where $p_i = n_i/N$ (n_i is the number of individuals of the ith taxon in the sample, and N is the total number of all individuals in the sample) and s = number of taxa. Equitability (E) was the second community structure index determined; E measures the proportional abundances among the various taxa in a sample (Krebs 1978) and ranges from 0.00 to 1.00, with 1.00 indicating all taxa in the sample are numerically equal. Equitability is expressed as:

$$E = H/\log_2 s$$

where H = Shannon-Wiener function and s = number of taxa. Both H and E were calculated for each sampling station.

Total benthic invertebrate densities, *Corbicula fluminea*, *Corophium* spp., and Ceratopogonidae (Diptera) larval densities, H, and E were each compared between areas (i.e., the ferry channel and reference area) and surveys using two-way analysis of variance (ANOVA) (Cruze and Hartzell 1991). Results from the two-way ANOVAs were used to determine significant ($P \leq 0.05$) impacts of the dredging project on benthic invertebrate densities, H, and E. Because sampling was conducted in the ferry channel and reference area prior to and after dredging, we were able to determine any significant impacts of the dredging by using the interaction term (survey x area) in the ANOVA. A significant interaction indicated a statistically significant effect of the dredging. Invertebrate densities were tested for normality, and, if necessary, transformed ($\log_{10}$) prior to performing ANOVA. Normality was tested by calculating normal scores of the data, then conducting a correlation test between the normal scores and the data (Cruze and Hartzell 1991). Mean densities of invertebrates from individual sampling stations provided the data for statistical tests.

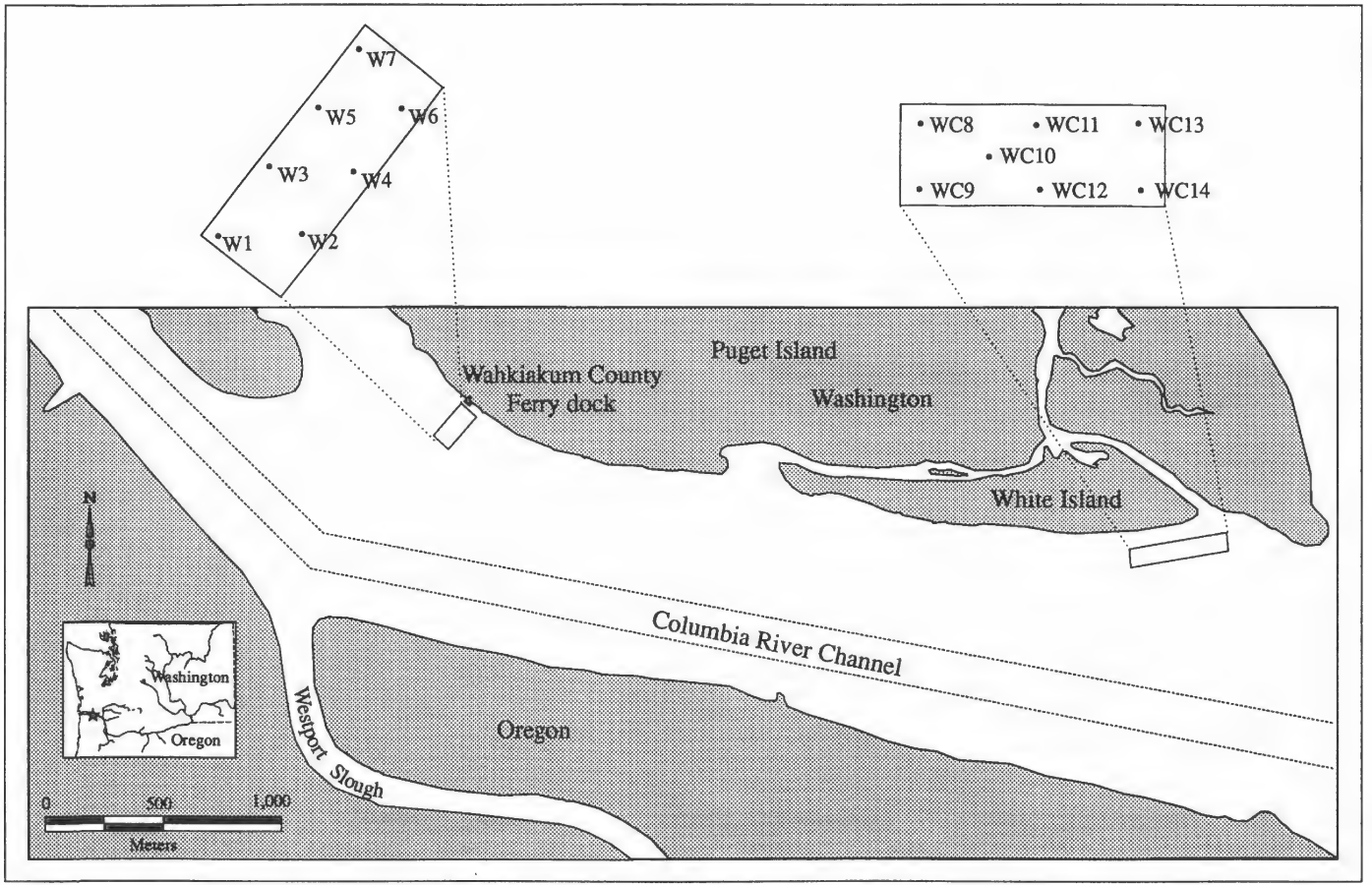


Figure 1. Locations of the Wahkiakum County Ferry Channel, Washington, and the upstream reference area. Locations of benthic invertebrate and sediment sampling stations in the dredged portion of the ferry channel and reference area are shown in the insets.

Median grain size and percent volatile solids of the sediment samples were each compared between areas (i.e., the ferry channel and reference area) and surveys using two-way ANOVA (Cruze and Hartzell 1991); median grain size and percent volatile solids were tested for normality and transformed ($\log_{10}$) prior to performing ANOVA. One low outlying value for median grain size (Station W3, July 1994) was removed prior to using ANOVA. No statistical comparisons for percent silt/clay were made because of the nonnormal distribution of the data and the lack of an adequate data transformation.

Results

Benthic Invertebrates

During all eight surveys, *Corbicula fluminea*, *Corophium* spp., and Ceratopogonidae larvae were generally the most common benthic invertebrates in both the ferry channel and the reference area (Table 1). In both areas, these three taxa represented 90% or more of the total benthic invertebrate densities during all surveys, except the July 1994 survey in the reference area. In both areas, *Corophium* spp. were generally the most abundant benthic invertebrates (Figure 2). We estimated that about 98% of the *Corophium* spp. were *C. salmonis* and the remainder *C. spinicorne*. The proportional abundances of *Corophium* spp. in the ferry channel ranged from 59% in July 1994 to 93% in January 1995; in the reference area, the proportional abundances ranged from 24% in July 1994 to 85% in January 1994.

The total numbers of taxa/categories collected in the ferry channel and reference area (data combined for both areas) ranged from 11 in April 1994 to 27 in October 1994. Mean numbers of taxa/categories (by survey) in the ferry channel and reference area were similar, ranging from 6 to 11 (Table 2).

The differences between areas for *Corbicula fluminea*, Ceratopogonidae larvae, *Corophium* spp., and total benthic invertebrate densities and H and E did not change over the surveys, indicating that the dredging did not have a statistically significant ($P \leq 0.05$) effect on these parameters (Table 3). All interaction terms (survey x area) in the analyses were nonsignificant ($P > 0.05$), indicating no effect of the dredging. Although we could not detect statistically significant effects of the dredging on benthic invertebrate densities, there appeared to be a potential dampening effect on invertebrates immediately after the dredging (Table 1). The dredging in the ferry channel did not appear to have any obvious impact on less common taxa found in the channel.

Corbicula fluminea, Ceratopogonidae larvae, and total benthic invertebrate densities were significantly different between surveys and areas (ANOVA, $P < 0.05$), with densities being significantly higher ($P < 0.05$) in the reference area than in the ferry channel (Tables 1 and 3). In the reference area, mean total benthic invertebrate densities (by survey) ranged from 2,291 organisms/m^2 in July 1994 to 25,266 organisms/m^2 in April 1994 (Table 1). Mean total benthic invertebrate densities (by survey) in the ferry channel ranged from 2,004 organisms/m^2 in February 1994 to 23,794 organisms/m^2 in January 1995. Mean *Corbicula fluminea* densities in the reference area ranged from 631 organisms/m^2 in April 1995 to 2,765 organisms/m^2 in April 1994 (Table 1), and mean densities in the ferry channel ranged from 194 organisms/m^2 in February 1994 to 1,360 organisms/m^2 in October 1994. In the reference area, mean densities of Ceratopogonidae larvae ranged from 521 organisms/m^2 in July 1994 to 2,159 organisms/m^2 in October 1994 (Table 1). Mean densities of Ceratopogonidae larvae in the ferry channel ranged from 396 organisms/m^2 in February 1994 to 1,116 organisms/m^2 in January 1994.

Corophium spp. densities, H, and E were significantly different between surveys (ANOVA, $P < 0.05$), but not between areas (ANOVA, $P > 0.05$) (Table 3). In the reference area, mean densities of *Corophium* spp. (by survey) ranged from 542 organisms/m^2 in July 1994 to 19,888 organisms/m^2 in April 1994 (Table 1). Mean densities in the ferry channel ranged from 1,364 organisms/m^2 in February 1994 to 22,157 organisms/m^2 in January 1995. Mean H values (by survey) in the reference area ranged from 1.02 in January 1994 to 2.22 in July 1994 (Table 2). In the ferry channel, mean H values (by survey) ranged from 0.84 in April 1995 to 1.85 in July 1994. Mean E values (by survey) in the reference area ranged from 0.34 in October 1994 to 0.70 in July 1994 (Table 2). In the ferry channel, mean E values (by survey) ranged from 0.30 in October 1994 to 0.61 in July 1994.

TABLE 1. Mean densities (number/m^2) of benthic invertebrates collected during eight surveys in Wahkiakum County Ferry Channel, Washington, and a reference area, 1993-1995. The ferry channel was dredged after the January 1994 survey and prior to the February 1994 survey.

Taxon/category	October 1993	January 1994	February 1994	April 1994	July 1994	October 1994	January 1995	April 1995
				FERRY CHANNEL				
Nemertea	2	0	0	0	14	106	55	170
Nematomorpha	0	0	0	0	0	0	0	0
Turbellaria	4	0	15	0	2	12	3	<1
Polychaeta								
Neanthes limnicola	0	0	0	0	1	1	0	1
Oligochaeta	27	94	16	121	29	1,074	68	220
Gastropoda	0	0	0	0	0	0	0	0
Lymnaeidae (unident. limpet)	0	0	0	0	0	1	0	0
Fluminicola virens	27	3	2	2	81	344	299	120
Juga plicifera	0	0	0	0	0	1	1	0
Bivalvia	0	0	0	0	0	1	0	0
Corbicula fluminea	510	392	194	445	289	1,360	642	398
Anodonta spp.	0	0	0	0	0	2	<1	0
Ostracoda	0	0	<1	3	4	22	2	18
Amphipoda								
Corophium spp.	3,342	8,565	1,364	3,836	1,427	16,509	22,157	12,171
Ramellogammarus spp.	0	0	0	0	0	0	0	0
Ramellogammarus oregonensis	2	1	0	11	0	2	4	23
Hyalella azteca	0	<1	0	0	0	1	1	0
Pontoporeia hoyi	0	0	0	0	0	1	0	0
Isopoda								
Gnorimosphaeroma oregonensis	0	0	0	0	1	0	0	0
Porcellio scaber	0	0	0	0	0	<1	0	0
Copepoda								
Harpacticoida	0	0	0	0	0	<1	0	0
Hydracarina	0	0	0	0	0	3	5	0
Insecta								
Collembola adult	<1	0	0	0	1	0	0	0
Plecoptera nymph	0	0	0	0	0	0	0	0
Ephemeroptera nymph	0	0	0	0	0	34	2	0
Odonata nymph	<1	0	0	0	0	11	<1	0
Hemiptera	0	0	0	0	0	0	0	0
Trichoptera larvae	0	0	0	0	0	<1	1	0
Coleoptera larvae	0	0	0	0	0	0	1	0
Miscellaneous Diptera								
Chironomidae larvae	20	14	16	57	71	158	21	17
Chironomidae pupae	1	0	0	0	34	2	<1	<1
Ceratopogonidae larvae	1,076	1,116	396	969	460	744	532	683
Total number/m^2	5,012	10,185	2,004	5,444	2,414	20,390	23,794	13,821

Continued, next page

TABLE 1. Continued

Taxon/category	October 1993	January 1994	February 1994	April 1994	July 1994	October 1994	January 1995	April 1995
				REFERENCE AREA				
Nemertea	4	0	9	<1	66	11	29	123
Nematomorpha	0	0	<1	0	0	0	0	0
Turbellaria	3	0	19	0	2	1	0	0
Polychaeta								
Neanthes limnicola	0	0	0	0	6	2	1	0
Oligochaeta	119	171	87	536	195	259	197	212
Gastropoda	7	0	0	0	0	0	0	0
Lymnaeidae (unident. limpet)	0	0	0	0	0	1	0	0
Fluminicola virens	78	114	84	78	243	348	131	43
Juga plicifera	0	<1	<1	0	0	<1	1	<1
Bivalvia	0	0	0	0	0	0	0	0
Corbicula fluminea	1,160	1,897	2,459	2,765	673	1,568	1,783	631
Anodonta spp.	0	0	0	0	0	0	0	0
Ostracoda	0	<1	0	<1	<1	0	0	0
Amphipoda								
Corophium spp.	2,448	19,822	14,869	19,888	542	17,127	17,084	9,277
Ramellogammarus spp.	2	0	0	0	0	0	0	0
Ramellogammarus oregonensis	0	19	56	13	1	3	4	4
Hyalella azteca	0	0	0	0	0	0	0	0
Pontoporeia hoyi	0	0	0	0	0	0	0	0
Isopoda								
Gnorimosphaeroma oregonensis	0	0	0	0	0	0	0	0
Porcellio scaber	0	0	0	0	0	0	0	0
Copepoda								
Harpacticoida	0	0	0	0	0	0	0	0
Hydracarina	0	0	0	0	0	0	0	0
Insecta								
Collembola adult	<1	0	0	0	<1	1	<1	0
Plecoptera nymph	0	0	<1	0	0	0	0	0
Ephemeroptera nymph	0	<1	<1	0	<1	0	3	0
Odonata nymph	0	0	0	0	0	0	0	0
Hemiptera	0	<1	1	0	0	0	0	0
Trichoptera larvae	0	0	0	0	0	0	0	0
Coleoptera larvae	0	0	0	0	0	0	<1	0
Miscellaneous Diptera								
Chironomidae larvae	31	93	80	329	20	26	17	16
Chironomidae pupae	2	0	<1	0	21	1	0	<1
Ceratopogonidae larvae	1,489	1,311	1,431	1,656	521	2,159	1,122	980
Total number/m^2	5,343	23,428	19,097	25,266	2,291	21,508	20,372	11,286

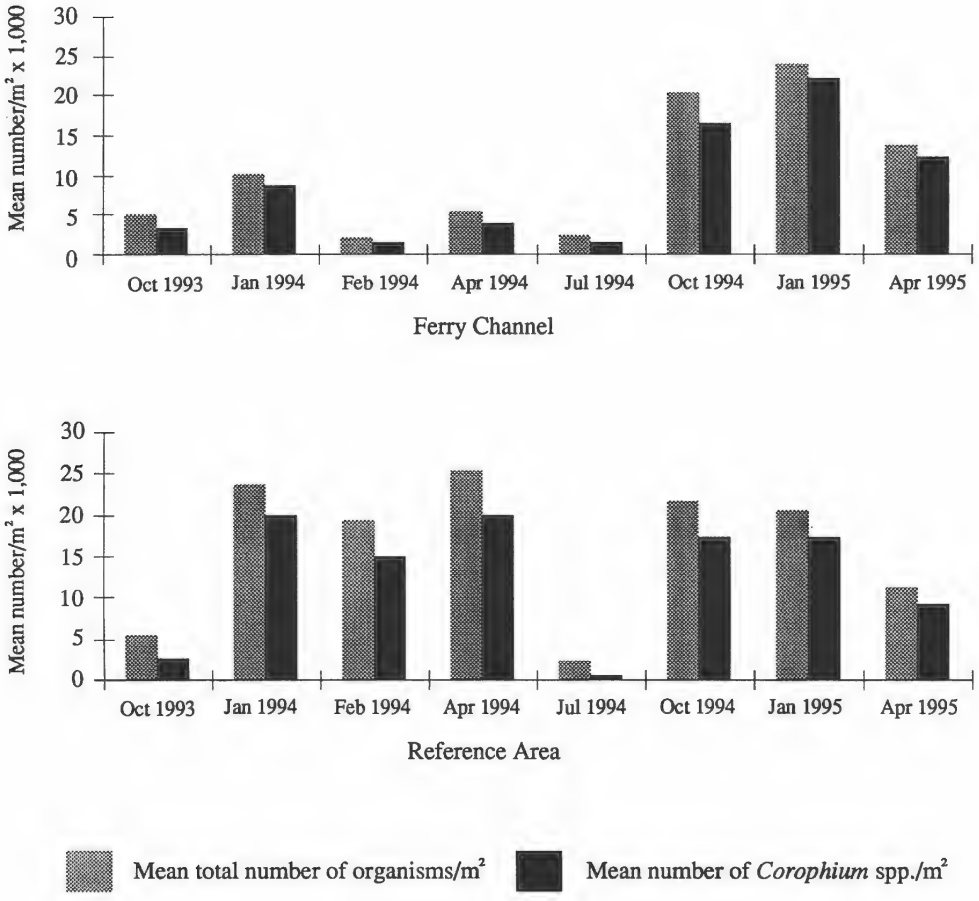


Figure 2. Mean densities of benthic invertebrates (total) and *Corophium* spp. in Wahkiakum County Ferry Channel, Washington, and a reference area, 1993-1995. The ferry channel was dredged after the January 1994 survey and prior to the February 1994 survey.

Sediments

Although median grain size was significantly smaller in the ferry channel than in the reference area (ANOVA, P = 0.00), no effect of the ferry channel dredging project on median grain size was detected in the statistical analysis, as indicated by the nonsignificant interaction (P = 0.88) between survey and area in the ANOVA. The overall means for median grain sizes in the ferry channel and reference area were 0.29 and 0.37 mm, respectively (Table 4). Median grain sizes were not significantly different between surveys (ANOVA, P = 0.18). Mean median grain sizes in the ferry channel ranged from 0.24 mm in July 1994 to 0.32 mm in January 1994, whereas in the reference area, mean median grain sizes ranged from 0.33 mm in January 1995 to 0.40 mm in October 1993 (Table 4).

The overall means for percents silt/clay in the ferry channel and reference area were 2.8 and 1.1%, respectively (Table 4). In the ferry channel, mean percents silt/clay ranged from 0.1% in January 1994 to 8.6% in July 1994. Mean percents silt/clay in the reference area ranged from 0.4% in October 1993 and January 1994 to 2.1% in April 1995.

TABLE 2. Mean numbers of benthic invertebrate taxa/categories identified and mean diversities (H) and mean equitabilities (E) calculated for benthic invertebrate samples collected during eight surveys in Wahkiakum County Ferry Channel, Washington, and a reference area, 1993-1995. The ferry channel was dredged after the January 1994 survey and prior to the February 1994 survey.

	October 1993	January 1994	February 1994	April 1994	July 1994	October 1994	January 1995	April 1995
				FERRY CHANNEL				
No. of taxa	7	6	6	6	8	11	9	7
H	1.34	1.07	1.25	1.26	1.85	1.03	1.03	0.84
E	0.49	0.43	0.47	0.50	0.61	0.30	0.38	0.32
				REFERENCE AREA				
No. of taxa	7	7	8	7	9	9	8	7
H	1.58	1.02	1.03	1.26	2.22	1.07	1.13	1.18
E	0.57	0.38	0.37	0.47	0.70	0.34	0.38	0.44

TABLE 3. Results of two-way analysis of variance for selected benthic invertebrate parameters measured in Wahkiakum County Ferry Channel, Washington, and a reference area, 1993-1995. Results from eight surveys—October 1993, January, February, April, July, and October 1994, and January and April 1995—were used in the analyses. A significant difference ($P \leq 0.05$) is indicated with an *.

Parameter	Source	Degrees of freedom	F	P value
Benthic invertebrate density (log_{10}), total	Survey	7	5.40	0.000*
	Area	1	6.23	0.014*
	Survey x area	7	1.90	0.078
	Total (deg. freedom)	111		
Corbicula fluminea density (log_{10})	Survey	7	2.39	0.027*
	Area	1	13.07	0.000*
	Survey x area	7	1.03	0.415
	Total (deg. freedom)	111		
Corophium spp. density (log_{10})	Survey	7	5.07	0.000*
	Area	1	0.25	0.615
	Survey x area	7	1.53	0.166
	Total (deg. freedom)	111		
Ceratopogonidae larvae density	Survey	7	3.39	0.003*
	Area	1	22.12	0.000*
	Survey x area	7	1.65	0.129
	Total (deg. freedom)	111		
Diversity (H)	Survey	7	11.76	0.000*
	Area	1	2.04	0.156
	Survey x area	7	1.00	0.438
	Total (deg. freedom)	111		
Equitability (E)	Survey	7	6.24	0.000*
	Area	1	0.35	0.554
	Survey x area	7	0.81	0.579
	Total (deg. freedom)	111		

No effect of the ferry channel dredging project on percent volatile solids was detected, as indicated by the nonsignificant interaction ($P = 0.56$) between survey and area in the ANOVA. Percents volatile solids were not significantly different between areas (ANOVA, $P = 0.45$) and, overall, averaged 0.6% in each area (Table 4). Percents volatile solids were significantly different between surveys (ANOVA, $P = 0.01$). In the ferry channel, mean percents volatile solids ranged from 0.5% in January 1994 to 0.8% in April 1994 (Table 4). In the reference area, mean percents

TABLE 4. Mean median grain sizes (mm), percents silt/clay, and percents total volatile solids of sediments sampled in Wahkiakum County Ferry Channel, Washington, and a reference area, 1993-1995. The ferry channel was dredged after the January 1994 survey and prior to the February 1994 survey.

	October 1993	January 1994	February 1994	April 1994	July 1994	October 1994	January 1995	April 1995
				FERRY CHANNEL				
Grain size (mm)	0.31	0.32	0.31	0.29	0.24	0.29	0.27	0.30
Silt/clay (%)	0.3	0.1	1.3	1.7	8.6	2.7	5.0	2.6
Vol. solids (%)	0.6	0.5	0.6	0.8	0.7	0.6	0.7	0.7
				REFERENCE AREA				
Grain size (mm)	0.40	0.37	0.39	0.38	0.39	0.36	0.33	0.35
Silt/clay (%)	0.4	0.4	1.7	1.0	0.9	0.5	1.6	2.1
Vol. solids (%)	0.6	0.6	0.6	0.8	0.6	0.5	0.5	0.7

volatile solids ranged from 0.5% in October 1994 and January 1995 to 0.8% in April 1994. Sediments from the ferry channel were tested for contaminants prior to the dredging project and were found to be uncontaminated (Jon Gornick, U.S. Army Corps of Engineers, Portland District, P.O. Box 2946, Portland, OR 97208. Pers. commun. 26 February 1996).

Discussion

The effects of dredging on benthic invertebrate communities vary widely. Morton (1977), who conducted a literature review of the ecological effects of dredging and dredge spoil disposal, noted that initial effects can range from negligible to severe and impacts range from short to long term. Based on his literature review, Morton (1977) concluded that short-term, small-scale dredging and dredge spoil disposal projects impacted benthic communities less than long-term, large-scale projects.

We were unable to detect any significant effect of the clamshell dredging project on the standing crops of benthic invertebrates in Wahkiakum County Ferry Channel. Apparently, benthic invertebrates in the dredged area were able to recolonize the area quite rapidly after dredging. In a study of the effects of dredging on benthic macroinvertebrates in a South Carolina estuary, Van Dolah et al. (1984) noted short-term effects of a dredging project, with substantial recovery within 3 months. They attributed much of the rapid recolonization to immigration via sediments of the slumping channel walls, which were similar to the sediments removed during dredging. Benthic invertebrates living in the slumping channel walls adjacent to Wahkiakum County Ferry Channel could have contributed to the rapid recolonization of the dredged area by benthic invertebrates. Although the sediments outside of the ferry channel were not sampled, we assume that they were similar to those removed from the ferry channel. If the sediments in slumping channel walls had been considerably different than those removed from the channel, then the benthos in the ferry channel may not have recovered as rapidly.

Corophium salmonis may also have migrated into the dredged channel from areas more distant than the slumping channel walls. Davis (1978) observed that *C. salmonis* actively migrated into the water column in the Columbia River estuary. *Corophium volutator*, a related Atlantic species, has been found to swim above the bottom during part of its life (Hughes 1988). If *C. salmonis* populations in the reach of the Columbia River near the Wahkiakum County Ferry Channel exhibit similar behavior, they could have been carried into the ferry channel by river currents. Muir (1990) found that *C. salmonis* was one of the three most abundant organisms collected in the drift along the bottom of the river downstream from Bonneville Dam.

No significant changes occurred in the benthic invertebrate community structure, as measured by H and E, in Wahkiakum County Ferry Channel as a result of the dredging project. Ideally, all benthic organisms should have been identified to the same taxonomic level, preferably species, for the community structure assessments; however, this was not practical or feasible given the financial constraints of the study. Even though different taxonomic levels of identification were used in

calculating both H and E, we believe our statistical comparisons are valid since similar taxonomic levels were used throughout the study.

Our study clearly demonstrates the need for at least one reference area in environmental assessments of dredging projects. Also, it is important to conduct sampling prior to dredging in both the impacted and reference areas. Underwood (1992) goes one step farther and states the need for multiple reference areas in environmental assessments, with sampling before and after in both the impact and reference areas. It is not practical or economically feasible to establish multiple reference areas in most benthic invertebrate studies. Without the data from the reference area, we would not have been able to make accurate conclusions regarding the impact of the dredging project on the benthos in the ferry channel. Samples collected in the reference area provided a means of assessing natural variation in the standing crops and community structure of benthic invertebrates in a specific reach of the lower Columbia River. Other researchers have noted that benthic invertebrate populations in other reaches of the lower Columbia River vary seasonally (Holton et al. 1984, McCabe and Hinton 1993, Hinton et al. 1995). In Grays Bay (RKm 37), Holton et al. (1984) observed that *Corophium salmonis* densities ranged from 4,122 organisms/m^2 in July 1981 to 31,754 organisms/m^2 in February 1981. Hinton et al. (1995) noted significant ($P < 0.05$) temporal differences in standing crops of benthic invertebrates (total), including *Corophium* spp., in a study area between Miller Sands and Pillar Rock Island, Columbia River estuary (RKm 40-42). In our study, densities of *Corophium* spp. fluctuated during the eight surveys, with the lowest overall density in July 1994.

In conclusion, we detected no significant effects ($P > 0.05$) of the ferry channel dredging project on benthic invertebrate densities or community structure from the statistical analyses of the data; however, there appeared to be a potential dampening effect on invertebrates in the ferry channel immediately after the dredging. In addition, we detected no significant effects ($P > 0.05$) of the dredging project on sediment median grain size or percent volatile solids.

Acknowledgements

We thank Lawrence Davis, Roy Pettit, Dennis Umphfres, Donald Gruber, and Nathan Cook for their assistance in collecting benthic samples during this study. Benjamin Sandford provided advice on the statistical analysis of the data. We thank Robert Hoffman for reviewing the manuscript. We appreciate the cooperation of the operators of the Wahkiakum County Ferry during our sampling efforts. The U.S. Army Corps of Engineers provided most of the funding for this study.

Literature Cited

Cruze, E., and B. Hartzell. 1991. Minitab reference manual, PC version, release 8. Quickset Inc., Rosemont, Pennsylvania.

Davis, J. S. 1978. Diel activity of benthic crustaceans in the Columbia River estuary. M.S. Thesis, Oregon State Univ., Corvallis. 170 pp.

Hinton, S. A., G. T. McCabe, Jr., and R. L. Emmett. 1995. In-water restoration between Miller Sands and Pillar Rock Island, Columbia River: environmental surveys, 1992-93. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-NWFSC-23. 47 pp.

Holton, R. L., D. L. Higley, M. A. Brzezinski, K. K. Jones, and S. L. Wilson. 1984. Benthic infauna of the Columbia River estuary. Final report on the benthic infauna work unit of the Columbia River Estuary Data Development Program. Oregon State Univ., Corvallis. 179 pp. plus appendices.

Hughes, R. G. 1988. Dispersal by benthic invertebrates: the *in situ* swimming behaviour of the amphipod *Corophium volutator*. J. Mar. Biol. Assoc. United Kingdom 68:565-579.

Kirn, R. A., R. D. Ledgerwood, and A. L. Jensen. 1986. Diet of subyearling chinook salmon (*Oncorhynchus tshawytscha*) in the Columbia River estuary and changes effected by the 1980 eruption of Mount St. Helens. Northw. Sci. 60(3):191-196.

Krebs, C. J. 1978. Ecology: the experimental analysis of distribution and abundance. Harper and Row. New York. 678 pp.

McCabe, G. T., Jr., R. L. Emmett, W. D. Muir, and T. H. Blahm. 1986. Utilization of the Columbia River estuary by subyearling chinook salmon. Northw. Sci. 60(2):113-124.

McCabe, G. T., Jr., and S. A. Hinton. 1993. Benthic invertebrates and sediments in vegetated and nonvegetated habitats at three intertidal areas of the Columbia River estuary, 1992. Final Rep. to U.S. Army Corps of Eng. by U.S. Natl. Mar. Fish. Serv., Seattle, Washington. 37 pp.

McCabe, G. T., Jr., W. D. Muir, R. L. Emmett, and J. T. Durkin. 1983. Interrelationships between juvenile salmonids and nonsalmonid fish in the Columbia River estuary. Fish. Bull., U.S. 81(4):815-826.

Morton, J. W. 1977. Ecological effects of dredging and dredge spoil disposal: a literature review. U.S. Fish Wildl. Serv. Tech. Pap. 94. 33 pp.

Muir, W. D. 1990. Macroinvertebrate drift abundance below Bonneville Dam and its relation to juvenile salmonid food habits. M.S. Thesis, Portland State Univ., Portland, Oregon. 40 pp.

Muir, W. D., and R. L. Emmett. 1988. Food habits of migrating salmonid smolts passing Bonneville Dam in the Columbia River, 1984. Regul. Rivers: Res. and Manage. 2:1-10.

Muir, W. D., R. L. Emmett, and R. J. McConnell. 1988. Diet of juvenile and subadult white sturgeon in the lower Columbia River and its estuary. Calif. Fish and Game 74(1):49-54.

Received 28 October 1997
Accepted for publication 2 March 1998

Underwood, A. J. 1992. Beyond BACI: the detection of environmental impacts on populations in the real, but variable, world. J. Exp. Mar. Biol. Ecol. 161:145-178.

U.S. Army Corps of Engineers. 1992. Westport, Oregon-Puget Island, Washington, Wahkiakum County Ferry Channel draft detailed project report, Section 107 study. U.S. Army Corps of Engineers, Portland District, P.O. Box 2946, Portland, Oregon. 33 pp. plus appendices.

Van Dolah, R. F., D. R. Calder, and D. M. Knott. 1984. Effects of dredging and open-water disposal on benthic macroinvertebrates in a South Carolina estuary. Estuaries 7(1):28-37.

Richard S. Zack, James Entomological Collection, Department of Entomology, Washington State University, Pullman, Washington 99164-6382

Shore Flies (Diptera: Ephydridae) of the Hanford Site, Washington

Abstract

Information is presented concerning the species composition, seasonal appearance, and habitat distribution of shore flies (Diptera: Ephydridae) at the Hanford Nuclear Site located in southcentral Washington State. The Hanford Site represents one of the largest undisturbed remnants of a shrub-steppe plant community in the western United States. Fifty-six species of shore flies in 32 genera were collected during the period 1994-1997. Aspects of the temporal distribution, relative abundance, and habitat selection of each species are discussed and compared to their appearance in the greater Pacific Northwest and with the results of a similar study conducted at Mount Rainier National Park which is located in the Cascade Mountain Range of central Washington. New distribution records for Washington are *Atissa litoralis*, *Hydrochasma faciale*, *Leptopsilopa varipes*, *Notiphila erythrocera*, *Philotelma alaskensis*, *Scatophila unicornis*, and *Trimerina madizans*. Because the Hanford Site was removed from public access and therefore widespread development in 1943, this study provides an understanding of the shore fly fauna that might have been common throughout the semi-arid, shrub-steppe region of central Washington before the advent of large-scale agriculture and urbanization.

Introduction

Shore flies (Ephydridae) constitute one of the most species-rich families of acalyptrate Diptera in North America. They are one of the more biologically diverse groups of flies, occurring in almost every aquatic habitat including fresh and alkaline waters, hot and cold mineral springs, and pools of crude petroleum. The world fauna was cataloged by Mathis and Zatwarnicki (1995). Worldwide, the family comprises over 1750 species, approximately 440 of which occur in America north of Mexico. Zack (1979, 1983a) surveyed the shore flies of Mount Rainier National Park which is located in the Cascade Mountain Range of Washington, and found 59 species in 22 genera in the physiographically and ecologically diverse habitats of the Park. Although not as ecologically diverse, consisting of several small spring systems and a single alkaline pond, the Hanford Site nonetheless yielded 56 species in 32 genera. In general, the shore fly fauna of Hanford is like that found throughout the central basins of Washington and Oregon and may represent a species composition that was characteristic of a much more widespread shrub-steppe habitat before the advent of large-scale agriculture and urbanization.

Located in the Pasco Basin of the southeast corner of the Columbia Plateau, primarily in northern Benton County, Washington, the Hanford Site comprises 560 square miles of predominantly shrub-steppe habitat administered by the United States Department of Energy. The land was acquired in 1943 as a national security area for the production of plutonium used in nuclear weapons. Most of the Site has been closed to the public since 1943. Today, Hanford is less known as a site of nuclear weapons development than for its international reputation in nuclear waste management, environmental restoration, and research and development.

From an ecological standpoint, the placing of such a large tract of land virtually off limits to public access for over half a century has preserved a shrub-steppe ecosystem that has otherwise changed radically throughout the surrounding Columbia Plateau. Hanford serves as a refuge for many plants and animals, including insects, that probably were once common throughout the Plateau but today are confined to remaining small, undisturbed tracts of land.

Climate at Hanford is best characterized as semi-arid with hot and dry summers and cold winters. Precipitation ranges from 30-35 cm at the crest of Rattlesnake Mountain (1150m) to less than 12 cm in central Hanford and along the Columbia River (150m). Temperature ranges from an average of 3°C in January to 33°C in July; temperatures of 32°C or above occur an average of 56 days per year (ERDA 1975).

In addition to general surveys (ERDA 1975, Rogers 1979), specific groups of insects studied at the Hanford Site include darkling beetles

© 1998 by the Northwest Scientific Association. All rights reserved.

(Rickard et al. 1974, Rickard and Haverfield 1965, Rogers et al. 1978), ground dwelling beetles (Rickard 1970), grasshoppers (Sheldon and Rogers 1978), torymid wasps (Grissell and Zack 1996), and weevils (O'Brien and Zack 1997). The vascular plants of Hanford, including details of the riparian flora, are found in Sackschewsky et al. (1992). Aspects of both flora and fauna are treated in Downes et al. (1993).

Materials and Methods

Shore flies were sampled using a standard 15 inch diameter fine-mesh, aerial insect net. In open, vegetation-free riparian and non-riparian areas, sweeping was conducted as close to the surface of the ground as possible. When disturbed, some groups of shore flies (e.g., *Atissa*, *Mosillus*, and *Parydra*) do not fly far in a vertical plane but will skim the surface in a horizontal direction. They can be difficult to collect if the net does not virtually touch the surface. In riparian areas with sparse vegetation along the shoreline or with low, emergent vegetation such as watercress, sweeping again took place as close to the surface of the water or ground as possible. When larger emergent plants such as cattail or sedges were present I tried to sweep through the vegetation. Species of *Notiphila*, especially, often perch on vegetation while other taxa such as *Ilythea* and certain *Parydra* are found at the ground surface between such plants. In any riparian area it is essential to completely sample all available microhabitats.

Sampling was not quantitative in design. In each habitat, flies were collected differentially from each of the microhabitats. Open riparian areas (e.g., the crust surrounding the alkaline pond) could be easily sampled in a minimal number of sweeps while heavily vegetated areas sometimes required the sight identification of flies on specific pieces of vegetation before they could be captured. In non-riparian grasses, shore flies usually were taken while sweeping for non-shore fly taxa, especially leafhoppers. The amount of time spent at each site during a given collecting period also varied depending on the availability of shore fly habitat due to events such as flooding and the presence or absence of seasonal vegetation.

After netting, flies were aspirated and placed into killing jars. Flies were eventually sorted, counted, and a representative sample prepared and deposited into the M. T. James Entomological Collection at Washington State University.

Table 1 indicates the general habitat type in which each species was encountered. I have defined the following broad habitat types at Hanford: 1. non-riparian vegetation; 2. alkaline pond; 3. spring/vegetation; and 4. spring/non-vegetation. Non-riparian vegetation consisted of areas, primarily with grasses, removed from surface waters by at least 500 m, that supported populations of shore flies. Within this habitat are species such as *Philygria debilis* Loew and *P. nigrescens* Cresson, the larvae of which probably feed on soil microorganisms, plant detritus, and possibly plant rootlets. Alkaline pond species are those found on the water surface of the pond or on the alkaline crust and vegetation-free or sparsely vegetated margins of the pond. The larvae of these species (e.g., *Mosillus bidentatus* (Cresson) and *Haloscatella muria* Mathis) probably feed on microorganisms including primarily algae and some decaying, wrack vegetation. Spring/vegetation species are most commonly associated with vegetation (e.g., sedges, cattails, and watercress) emerging from the water or immediately adjacent to it. Larvae of these taxa (e.g., *Notiphila* and *Hydrellia*, see Deonier 1971) are primarily phytophagous feeding on the roots and stems of those plants. Spring/non-vegetation species are found in vegetation free or sparsely vegetated outflow areas surrounding the springs themselves. At Hanford, the largest of these systems was Rattlesnake Spring. Taxa found in this habitat include certain *Scatella*, *Parydra*, *Atissa*, and *Discocerina*. Larvae of these species feed on microorganisms, primarily algae, and possibly some decaying vegetation. In this habitat, the presence and abundance of a given species may fluctuate dramatically based on the amount of available habitat which is subject to changes due primarily to periodic flooding.

As in previous studies (Scheiring and Foote 1973, Zack 1979, 1983a), the relative abundance of each species is calculated based on its percentage of the total number of specimens taken within each of the four designated habitats. In all situations where only a single specimen was taken, the species is listed as rare (Table 1). Abundance figures were designated as follows:

rare (r)	0-3 percent of the total catch/habitat
occasional (occ)	3-9 percent
common (c)	9-15 percent
abundant (a)	15-26 percent
very abundant (va)	26 percent and greater

TABLE 1. Species inventory, habitats, relative abundance, and months during which individual species were collected.

Species	Habitat Type and Relative Abundance	Months Species was Collected
Subfamily Discomyzinae		
Leptopsilopa varipes (Coquillett)*	spring/vegetation (occ)**	Mar, Sep
Psilopa compta (Meigen)	spring/vegetation (occ)	Mar, Apr, May, Jun, Jul, Aug, Oct
P. girschneri von Röder	spring/vegetation (occ) non-riparian vegetation (r)	Apr, Jun, Aug, Oct
Trimerina madizans (Fallén)*	spring/vegetation (r)	Jun
Subfamily Hydrellinae		
Atissa litoralis (Cole)*	spring/non-vegetation (r)	May, Jun, Oct
Hydrellia griseola (Fallén)	spring/vegetation (a) non-riparian vegetation (c)	Mar, Apr, May, Jun, Jul, Aug, Sep, Oct
H. proclinata Cresson	spring/vegetation (a)	May, Jun, Jul, Aug
H. sp. 1	spring/vegetation (r)	Mar, May, Jun, Aug, Oct
H. sp. 2	spring/vegetation (r)	Aug, Oct
H. sp. 3	spring/vegetation (r)	May
Notiphila aenegma Cresson	spring/vegetation (occ)	May, Jun, Aug
N. decoris Williston	spring/vegetation (r)	Jun, Jul, Aug, Oct
N. erythrocera Loew*	spring/vegetation (r)	Jun, Aug, Oct
N. macrochaeta Loew	spring/vegetation (r)	May, Jun, Jul, Aug, Oct
N. olivacea Cresson	spring/vegetation (occ)	May, Jun, Aug
N. quadrisetosa Thomson	spring/vegetation (r)	May, Jun, Jul, Aug, Oct
Ptilomyia alkalinella (Cresson)	alkaline pond (occ)	Jun
Typopsilopa arnaudi Wirth*	spring/vegetation (occ)	Mar, Jun, Jul, Aug, Oct
Subfamily Gymnomyzinae		
Allotrichoma sp.	spring/non-vegetation (occ) non-riparian vegetation (r)	Mar, Apr, May, Jun, Jul, Aug, Oct
Diclasiopa lacteipennis (Loew)	spring/non-vegetation (r)	Jul
Discocerina obscurella (Fallén)	spring/non-vegetation (occ)	May, Jul, Aug
Gymnoclasiopa argyrostoma (Cresson)	spring/non-vegetation (occ) non-riparian vegetation (r) alkaline pond (r)	Mar, Apr, May, Jun, Jul, Aug
Hydrochasma faciale (Williston)	spring/non-vegetation (r)	Jul
Mosillus bidentatus (Cresson)	spring/non-vegetation (occ) alkaline pond (occ)	Apr, Jun
M. tibialis Cresson	spring/non-vegetation (c)	May, Jun, Jul, Sep
Ochthera anatolikos Clausen	spring/non-vegetation (r)	Jun
O. occidentalis Clausen	spring/non-vegetation (r) spring/vegetation (r)	Jun, Jul, Aug
Polytrichophora setigera (Cresson)	spring/non-vegetation (r)	May
Subfamily Ilytheinae		
Hyadina binotata (Cresson)	spring/non-vegetation (r) spring/vegetation (r)	Mar, May, Jun, Jul
Ilythea caniceps Cresson	spring/vegetation (r)	Mar, May, Jul, Sep
Lytogaster gravida Loew	spring/non-vegetation (r) spring/vegetation (r)	Mar, May, Jun, Jul, Aug, Sep, Oct
Nostima picta picta (Fallén)	spring/vegetation (r)	Apr, Aug
Philygria debilis Loew	spring/vegetation (occ) non-riparian vegetation (a)	Mar, Apr, May, Jun, Jul, Aug, Sep, Oct
P. nigrescens (Cresson)	spring/vegetation (r) non-riparian vegetation (occ)	May, Jun, Jul, Aug, Sep
Pelina prospinosa Clausen	spring/vegetation (r)	Mar, Jul, Oct

Table 1 Continued, next page

TABLE 1. Continued

Species	Habitat Type and Relative Abundance	Months Species was Collected
Subfamily Ephydrinae		
Calocoenia platypelta (Cresson)	spring/vegetation (r)	Oct
Ephydra packardi Wirth	spring/non-vegetation (r)	Aug
Haloscatella arichaeta (Mathis)	spring/non-vegetation (occ) alkaline pond (occ)	May, Jun, Jul
H. muria (Mathis)	spring/non-vegetation (occ) alkaline pond (r)	May, Jun, Jul, Aug
Lamproscatella occidentalis Mathis	spring/non-vegetation (a) non-riparian vegetation (occ)	Mar, Apr, May, Jun, Oct
Limnellia turneri Mathis	spring/vegetation (occ) non-riparian vegetation (r)	Mar, May, Jun, Sep, Oct
Paracoenia bisetosa (Coquillett)	spring/non-vegetation (occ) alkaline pond (va)	Mar, Jun, Jul
Parydra aquila (Fallén)	spring/non-vegetation (r)	May, Jun, Jul
P. aurata Jones	spring/non-vegetation (r)	Mar, Jun, Jul, Aug
P. fossarum (Haliday)	spring/non-vegetation (a)	Mar, May, Jun, Jul, Aug, Oct
Philotelma alaskensis Cresson*	spring/non-vegetation (r)	May
Scatella marinensis (Cresson)	spring/vegetation (r)	Mar, Apr, May, Jun, Aug
S. paludum (Meigen)	spring/vegetation (occ) spring/non-vegetation (va)	May, Jun, Jul, Aug, Oct
S. stagnalis (Fallén)	spring/vegetation (a) spring/non-vegetation (va)	Mar, Apr, May, Jun, Jul, Aug, Sep, Oct
S. triseta Coquillett	spring/vegetation (r)	Mar, May, Jun, Jul
Scatophila despecta (Haliday)	spring/vegetation (occ) spring/non-vegetation (a)	Mar, Apr, May, Jun, Jul, Aug, Sep, Oct
S. exilis Cresson	spring/vegetation (r) spring/non-vegetation (r)	Mar, Apr, May, Jun, Jul, Oct
S. unicornis Czerny	spring/vegetation (r)	May
S. sp. 1	spring/vegetation (r)	Apr
S. sp. 2	spring/vegetation (r)	Mar
S. sp. 3	spring/vegetation (r) spring/non-vegetation (r)	Mar, Apr, May
S. sp. 4	spring/vegetation (r)	May
Setacera aldrichi Cresson	spring/vegetation (r)	Oct
S. needhami Johannsen	spring/non-vegetation (r)	Oct
S. pacifica (Cresson)	spring/non-vegetation (r)	Mar

*indicates a new distribution record for Washington State (Mathis and Zatwarnicki 1995)

**Letters indicate relative abundance: va=very abundant, a=abundant, c=common, occ=occasional, r=rare (see text for explanation)

Temporal differences are not taken into account in these abundance designations but presence during seasonal periods can be obtained from the discussion of each species found in the Results section of this paper. Shore flies were sampled at the Hanford Site 36 times during the four year period. However, not all sites were sampled during each visit and the apparent absence of a species during seasonal periods should not be taken as an indication that the species was not present. Based on numerous systematic and distributional studies (see for example, Zack 1979, 1983a, Deonier 1965, Scheiring and Foote 1973, as well as revisional studies cited in this paper) most shore fly species are multivoltine with no seasonal breaks in occurrence given the availability of appropriate habitat. Since many aquatic habitats, especially small spring systems and alkaline ponds which made up the majority of habitats on the Hanford Site, are subject to dramatic changes throughout the year, one would expect shore fly populations and species composition to fluctuate depending

on the frequency and severity of environmental factors such as precipitation. Observationally, this was the situation at Hanford.

Survey Sites

Administratively, Hanford is divided into several subunits. Two of these subunits were surveyed during this study. The first is often referred to as central Hanford. This area is bordered by the Columbia River to the north and east, Route 24 to the northwest, and the Fitzner-Eberhardt Arid Lands Ecology Reserve (ALE) to the west. The Arid Lands Ecology Reserve was the second subunit surveyed. ALE is an area of approximately 75,000 acres that lies to the south and west of central Hanford. ALE runs north and east from the summit of Rattlesnake Ridge (1150 m) to the Cold Creek Valley (150 m). Fourteen intermittent and permanent springs occur on ALE; these are the only lotic habitats, aside from the Columbia River, that occur at Hanford.

Three sites on central Hanford yielded shore flies. While the Hanford Site contains a long stretch of free-flowing Columbia River, only one site along the River was surveyed and this was on just two occasions. The Columbia River pumping station site lies along the River near the Washington Public Power Supply System nuclear energy generating plants approximately 20 km north of Richland. Rocky areas along the River and small pools adjacent to it were swept for flies. The site along the River was generally unproductive for shore flies.

The only naturally occurring pond on the Hanford Site is West Lake. This alkaline pond is situated at the west end of Gable Mountain. West Lake is surrounded by an alkaline crust with no emergent macrovegetation along the shoreline. However, large areas of bulrush (*Scirpus* spp.) and various grasses and other vegetation occur in the area surrounding the pond. The size of the pond is a direct function of groundwater elevation and fluctuates throughout long and short term periods depending on climate and seasonal weather conditions. On average, the pond encompasses ten acres. Because the pond is not referred to as "West Lake" on any topographic maps, I chose to label the insects as collected at an "alkaline pond." This is the designation that appears in the Results section of this paper and on specimen labels.

A large area of sand dunes exists along the western margin of the Columbia River and several kilometers inland. The dunes were sampled extensively for various taxa. Shore flies were not a target of these surveys but were collected on two occasions by sweeping sand dune vegetation. Only *Psilopa girschneri* von Röder, *Philygria debilis* Loew, and *Allotrichoma* sp. were taken at this site. These species may have been collecting plant nectar as a food source.

Shore flies were collected from nine sites on ALE, although three of these sites were not riparian. The radio telescope site is located at the southeast corner of Rattlesnake Ridge and primarily consists of a big sagebrush (*Artemisia tridentata* Nutt.)/bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scrib. & Smith) plant community. Other equivalent, non riparian survey sites along the Ridge are listed as Rattlesnake Ridge in discussions of species. The third non-riparian site is recorded as the 1200 Foot Road. This was a dirt access road, with abundant adventitious vegetation, located at approximately 360 m (1200 ft) in elevation at the southeast base of Rattlesnake Ridge. Collecting at all of these sites involved general sweeping of vegetation as shore flies were not expected to be common.

Fourteen intermittent and permanent springs have been mapped on ALE; four of these systems were sampled during this study. The site designated Rattlesnake Ridge/spring is an unnamed spring that occurs just below the summit of the Ridge on the northeast facing slope. This spring consisted of a small pool approximately one meter in diameter and a cascading flow that traveled 10-15 meters before it disappeared into the soil. Several small, shrubby willows (*Salix* spp.) grow along the margins of the spring and stream providing some shade while sedge (*Carex* spp.) and cattail (*Typha latifolia* L.) grew sparingly.

The Rattlesnake Spring system is situated in the northwest corner of ALE on the flat of Cold Creek Valley. This is the most prominent, permanent spring on the Hanford Site and flows for about 3 km, beginning from ground seepage and being fed by a number of smaller springs along its course. Eventually it disappears into the ground. The bottom of the stream is composed of sand and gravel. The system is subject to periodic flash floods, especially in the winter and spring, that may completely scour sections of the stream form-

ing areas of vegetation-free shoreline. Over 90 species of algae and diatoms have been recorded from the system (ERDA 1975) but the dominant macrophyte is watercress (*Rorippa nasturium-aquatica* (L.) Schinz & Thell.) which seasonally occupies as much as 85% of the stream area (ERDA 1975). Cattail and sedges are common along the stream margin. Peachleaf willow (*Salix amygdaloides* Anders.) is the dominant tree throughout the Rattlesnake Spring corridor.

Lower Snively Spring (including the sites designated below Lower Snively Spring and Snively Ranch) is another large spring system occurring in Snively Canyon which lies south of Rattlesnake Spring. This system runs approximately 2 km down Snively Canyon. In addition to vegetation discussed for Rattlesnake Spring, shrubby willows, mockorange (*Philadelphus lewisii* Pursh), and black cottonwood (*Populus trichocarpa* T. & G.) dominate the spring corridor.

Bobcat Spring lies in lower Bobcat Canyon which is located at the base of Rattlesnake Ridge in central ALE. This is a spring system consisting of a small pool 5-6 meters in diameter with a short-lived outflow which eventually disappears into the ground. Although a thick margin of shrubs surround the spring, there is no extensive canopy and the spring and stream are usually choked with watercress.

Distributional information is taken primarily from Mathis and Zatwarnicki (1995). Species indicated as new for Washington are not recorded in their catalog as occurring in the state. Dates listed for a species collection should not be interpreted as inclusive or an indication that the species was not at a survey site at other time periods. Not all sites were collected on a systematic basis; some more remote sites were sampled only 4-5 times during the survey while other more accessible sites were sampled as many as 20 times. The following arrangement follows that in Mathis and Zatwarnicki (1995) except that species are arranged alphabetically within subfamilies. When available, I have included biological information.

Results

Subfamily Discomyzinae

Leptopsilopa varipes (Coquillett). New WA record; 28 Mar, 15 Sep. Rattlesnake Ridge/spring, Bobcat Canyon. *Leptopsilopa varipes* is a western species previously recorded from British Columbia, California, and Idaho. The fact that the species was collected only in the early spring and late summer probably does not indicate that it is a spring/fall species.

Psilopa compta (Meigen). 22 Mar, 29 Mar, 11 Apr, 24 Apr, 3 May, 1 Jun, 21 Jun, 20 Jul, 5 Aug, 11 Oct. Rattlesnake Spring, Lower Snively Spring, Snively Ranch, Bobcat Canyon. Found throughout the Afrotropical, and Holarctic Regions, this is a common species throughout the Pacific Northwest, especially in habitats with extensive shoreline vegetation. At Mount Rainier (Zack 1979, 1983a), it was the most abundant species in the sedge meadow habitat. Throughout eastern Washington, *P. compta* is extremely common in both the sedge meadow and cattail marsh habitats. Zack (1983a) presented information on the biology of this fly.

Psilopa girschneri von Röder. 20 Apr, 10 Jun, 21 Jun, 5 Aug, 29 Aug, 11 Oct. Rattlesnake Spring, Lower Snively Spring, Rattlesnake Ridge/spring, sand dunes. *Psilopa girschneri* is found throughout much of the world. One specimen was taken at Mount Rainier in the sedge meadow habitat (as *Psilopa olga* Cresson). At Hanford, it was found to be sympatric with *P. compta* at most sites on most dates. Throughout eastern Washington, it can be found with *P. compta*, often abundantly.

Trimerina madizans (Fallén). New WA record; 21 Jun. Rattlesnake Spring. This Holarctic species was previously reported from several northeastern states and Quebec and as far west as Iowa and Ohio. Only one specimen was collected on the Hanford Site. I have collected the species from southern (Hart Mountain Wildlife Refuge, Lake County) and northcentral Oregon (McNary Wildlife Area, Umatilla County) as well as at three locations in eastern and central Washington. The species has never been found in abundance, and no more than two specimens have been taken at any location. All specimens were taken while sweeping thick vegetation surrounding springs or small pools.

Subfamily Hydrelliinae

Atissa litoralis (Cole). New WA record;16 May, 21 Jun, 11 Oct. Rattlesnake Spring, Lower Snively Spring. Previously reported from California and Oregon in the west and Ohio and Iowa in the midwest. Only four specimens were collected. I

have collected this species at several sites throughout eastern Washington, primarily on vegetation-free shorelines of small pools.

Hydrellia griseola (Fallén). 29 Mar, 19 Apr, 20 Apr, 3 May, 15 May, 16 May, 1 Jun, 10 Jun, 21 Jun, 7 Jul, 12 Jul, 20 Jul, 31 Jul, 5 Aug, 19 Aug, 29 Aug, 1 Sep, 11 Oct. Rattlesnake Spring, Lower Snively Spring, below Lower Snively Spring, Bobcat Canyon, Rattlesnake Ridge/spring, radio telescope, Columbia River pumping station.

H. griseola was collected in numerous aquatic and nonaquatic habitats throughout the Hanford Site. The species was abundant throughout the field season. *H. griseola* is nearly cosmopolitan and is occasionally considered a pest of rice; Mathis and Zatwarnicki (1995) presented an extensive list of host plants. Although abundant in and around riparian situations where the larvae bore stems of aquatic vegetation, adults are also found considerable distances from water where they visit flowers and feed on plant nectar. At Hanford, most specimens were taken by sweeping riparian vegetation. However, the species was not uncommon in meadow and grassy areas far removed from water. Although nectaring sources often were not identified, several specimens were taken from the flowers of meadow goldenrod, *Senecio canadensis* L.

This is one of the most commonly collected northwestern shore flies; it is certainly the most common in areas with substantial riparian vegetation, but it also occurs on shorelines with extensive non-vegetated areas where adults probably feed on algae and other microorganisms. At Mount Rainier, *H. griseola* was collected in seven of 10 habitat types sampled and was very abundant on flower heads of pearly-everlasting [*Anaphalis margaritacea* (L.) B&H] (Zack 1979, 1983a). While shore fly/flowering plant associations are reported elsewhere in the literature (Deonier 1971; Scheiring and Foote 1973; Judd 1977) they are, nonetheless, rare.

Hydrellia proclinata Cresson. 3 May, 1 Jun, 7 Jul, 12 Aug, 29 Aug. Rattlesnake Spring, Lower Snively Spring, below Lower Snively Spring, Rattlesnake Ridge/spring. This common species is found throughout most of the western United States and western Canada. It is often taken in conjunction with *H. griseola*. At Mount Rainier, the species was found in several habitat types, but was most common in vegetation of roadside ditches (Zack 1979, 1983a). At both Mount Rainier and Hanford it was not found in meadows or visiting flowers as was *H. griseola*.

Hydrellia is a species-rich taxon last revised by Deonier (1971). Species are sometimes difficult to identify and numerous new species, especially in the Pacific Northwest fauna, have been recognized but not yet described. I chose not to apply names to the following three species at this time. Although they appear related to described species with northwestern distributions, differences in morphology and genitalia indicate that some species may be more variable than previously defined or that these are new species. Continuing faunistic and systematic studies should help to clarify these situations. Intensive collecting of often host-plant specific and therefore habitat-specific *Hydrellia* is needed.

Hydrellia sp. 1. 29 Mar, 16 May, 21 Jun, 19 Aug, 11 Oct. Rattlesnake Spring, Lower Snively Spring.

Hydrellia sp. 2. 29 Aug, 11 Oct. Rattlesnake Spring.

Hydrellia sp. 3. 16 May. Rattlesnake Spring.

Notiphila aenigma Cresson. 3 May, 16 May, 1 Jun, 21 Jun, 5 Aug, 19 Aug, 29 Aug. Rattlesnake Spring, Lower Snively Spring, Rattlesnake Ridge/spring. This species occurs throughout the western United States and southwestern Canada. It was the second most abundant *Notiphila* (next to *N. quadrisetosa*) collected on the Hanford Site and is one of the most commonly collected species in the central basin of Washington. Mathis (1979) and Busacca and Foote (1978) discussed the biology of this species. The latter paper also contains descriptions of the immature stages. Two specimens of *N. aenigma* were collected at Mount Rainier, one each in the sand shore and sedge meadow habitats (Zack 1979, 1983a).

Notiphila decoris Williston. 21 Jun, 20 Jul, 19 Aug, 29 Aug, 11 Oct. Rattlesnake Spring. Like all other species of *Notiphila*, *N. decoris* was swept from emergent vegetation around the margin of a permanent spring. This is a common species throughout eastern Washington and eastern Oregon and is often found sympatrically with *N. macrochaeta*.

Notiphila erythrocera Loew. New WA record. 10 Jun, 21 Jun, 5 Aug, 19 Aug, 29 Aug, 11 Oct. Rattlesnake Spring. This species is Neotropical and Nearctic in distribution; it occurs throughout

most of the United States. It appears, however, to reach its northern limit in Washington where it is here recorded for the first time. Although it was collected throughout the season, I never found more than one or two individuals at any site during a day's collecting activities. It was always taken in conjunction with other species of *Notiphila*. During intensive collecting throughout Washington, this is the only known location where *N. erythrocera* occurs.

Notiphila macrochaeta Loew. 3 May, 1 Jun, 7 Jul, 5 Aug, 19 Aug, 29 Aug, 11 Oct. Rattlesnake Spring. Mathis (1979) states that *N. macrochaeta* is often taken with specimens of *N. olivacea* and *N. decoris*. This was certainly the case at Hanford where the three species were taken together in almost all collections.

Notiphila olivacea Cresson. 3 May, 16 May, 1 Jun, 21 Jun, 5 Aug. Rattlesnake Spring. This is one of the most commonly collected *Notiphila* in the Pacific Northwest. I have collected it throughout the central basin of Washington in vegetation, especially sedges, around the margins of both fresh and slightly alkaline ponds.

Notiphila quadrisetosa Thomson. 3 May, 16 May, 1 Jun, 10 Jun, 21 Jun, 7 Jul, 5 Aug, 19 Aug, 29 Aug, 11 Oct. Rattlesnake Spring, Lower Snively Spring, below Lower Snively Spring. *Notiphila quadrisetosa* is widely distributed and commonly collected in Washington; the Hanford Site is no exception.

Ptilomyia alkalinella (Cresson). 27 Jun. Alkaline pond. This western species is a common component of the fauna occurring on the vegetation free margins of alkaline ponds throughout central Washington. At Hanford, specimens were taken only at the alkaline pond.

Typopsilopa arnaudi Wirth. New WA record; 22 Mar, 1 Jun, 7 Jul, 5 Aug, 19 Aug, 29 Aug, 11 Oct. Rattlesnake Spring and Bobcat Canyon. This species is known from throughout the western United States and south to Baja California Norte in Mexico. I have collected it at several other locations in southcentral Washington, but not in northern Washington or in southern British Columbia. The basin area of southcentral Washington may represent its northernmost occurrence.

Subfamily Gymnomyzinae

Allotrichoma sp. 29 Mar, 11 Apr, 20 Apr, 24 Apr, 16 May, 1 Jun, 10 Jun, 21 Jun, 7 Jul, 20 Jul, 29 Aug, 11 Oct, Rattlesnake Spring, Lower Snively Spring, below Lower Snively Spring, Snively Ranch, Rattlesnake Ridge/spring, sand dunes. *Allotrichoma* and related genera have a long and complicated taxonomic history. Species are difficult to define and numerous undescribed species certainly exist. *Allotrichoma* is a common component of the northwestern shore fly fauna and is especially abundant in the central basins of Washington and Oregon. The genus is in need of revision.

Diclasiopa lacteipennis (Loew). 12 Jul. Rattlesnake Spring. Only one specimen of this species was collected at Rattlesnake Spring. *Diclasiopa lacteipennis* occurs in the Afrotropical, and Holarctic Regions and is found along vegetation free shorelines of most central Washington streams and small pools.

Discocerina obscurella (Fallén). 3 May, 16 May, 31 Jul, 19 Aug. Rattlesnake Ridge/spring, Rattlesnake Spring, Lower Snively Spring. This is one of the most widespread species of shore fly occurring in the Afrotropical, Neotropical, and Holarctic Regions. It is a very common component of mud and sand shore habitats throughout the Pacific Northwest. Zack (1979, 1983a) found *D. obscurella* in the moist meadow and mud and sand shore habitats at Mount Rainier National Park. The biology and immature stages of this species were treated by Foote and Eastin (1974).

Gymnoclasiopa argyrostoma (Cresson). 29 Mar, 11 Apr, 15 May, 16 May, 9 Jun, 10 Jun, 27 Jun, 7 Jul, 8 Jul, 12 Aug, 19 Aug. Rattlesnake Spring, Lower Snively Spring, Snively Ranch, Rattlesnake Ridge/spring, alkaline pond, radio telescope, Rattlesnake ridge. This was one of the most commonly encountered species on the Hanford Site, being collected in both aquatic and nonaquatic situations. It is one of the few species of shore fly that is found in grasslands and meadows, often a considerable distance from water. It is not known if larvae live and feed in the soil of these habitats or if adult flies travel from more normal shore fly aquatic and semi-aquatic breeding and larval sites. In aquatic situations, adults are common on open mud and sand shores.

The species has a sporadic distribution in the western United States and Saskatchewan, Canada. It is one of the most commonly encountered species in Washington and the Pacific Northwest; it was found in seven of 10 habitat types surveyed

at Mount Rainier (Zack 1979, 1983a) and was very common in the wet woodland and sand shore habitats. It was also very abundant on the flowers of *Anaphalis margaritacea* (L.) B&H and travels from aquatic habitats in search of plant nectar (see discussion of *Hydrellia griseola*).

Hydrochasma faciale (Williston). New WA record. 12 Jul, 20 Jul, 31 Jul. Rattlesnake Spring. This species is primarily Neotropical in distribution with previous Nearctic records from California, Arizona, and Texas. The species probably occurs throughout much of the more arid central basin of western North America. Southcentral Washington may represent its northern limit. Collected only in July, the species may have a limited temporal distribution.

Mosillus bidentatus (Cresson). 11 Apr, 20 Jun, 28 Jun. Rattlesnake Spring, Lower Snively Spring, alkaline pond. This species is known from throughout the western and central United States where it can be abundant along vegetation-free shore margins of ponds and streams. It is especially prevalent along the margins of alkaline ponds, as it is at Hanford. Mathis et al. (1993) revised *Mosillus* and present short discussions of this and the following species.

Mosillus tibialis Cresson. 16 May, 1 Jun, 10 Jun, 21 Jun, 7 Jul, 8 Jul, 20 Jul, 1 Sep. Rattlesnake Spring, below Lower Snively Spring, Rattlesnake Ridge/spring. This widely distributed species is found throughout the United States and southern British Columbia to sites in Central and South America. Like *M. bidentatus*, this species is more commonly found along vegetation-free margins of ponds and springs. In extensive collecting throughout the central basin of Washington, it appears that *M. tibialis* is more prevalent in fresh to slightly alkaline situations while *M. bidentaus* is more common in moderately to highly alkaline situations. Both species, however, are most often associated with wrack vegetation and this may be where eggs are deposited and larvae feed. Mating is often observed on this wrack debris.

Ochthera anatolikos Clausen. 1 Jun. Lower Snively Spring. One male specimen of this species was collected on the Hanford Site. This is one of the most widespread species of *Ochthera,* occurring throughout most of the United States and Canada, and being especially common in the northeast. It has been found throughout Washington.

Ochthera occidentalis Clausen. 1 Jun, 7 Jul, 5 Aug. Lower Snively Spring. *Ochthera occidentalis* is found primarily in the western United States and western Canada. This species also occurs throughout Washington, and one specimen was collected at Mount Rainier (Zack 1979, 1983a). *Ochthera occidentalis* is the most commonly collected *Ochthera* in central Washington.

Ochthera females. Several species of *Ochthera* often occur sympatrically at single locations, and females are difficult if not impossible to separate. While specimens included in this category probably include the two species thus far identified from the Hanford Site, it is possible that other species, including *O. collina* Clausen which also occurs in the central basin of Washington, occur at Hanford. All *Ochthera* are predaceous as both adults and immatures and can be found in almost all aquatic habitats where they prowl both open riparian areas as well as shore line vegetation searching for prey. The genus was revised by Clausen (1977).

Polytrichophora setigera (Cresson). 16 May. Lower Snively Spring. Only two specimens were taken at the Hanford Site. *Polytrichophora setigera*, however, is a common inhabitant of pond and slow moving stream margins throughout the central basin of Oregon and Washington. It occurs mainly in riparian areas devoid of vegetation.

Subfamily Ilytheinae

Hyadina binotata (Cresson). 29 Mar, 16 May, 1 Jun, 21 Jun, 7 Jul. Rattlesnake Spring, Lower Snively Spring. The species appears to have a widespread but spotty distribution with records from Alaska in the west to Georgia and Ohio in the East, to Mexico in the south. Additional studies will probably fill many of these distributional gaps. Zack (1979, 1983a) found the species to be a rare inhabitant in the moist meadow, mud shore, and sand shore habitats. Clausen (1983), in his revision of the genus, records *H. binotata* as a common northwestern species.

Ilythea caniceps Cresson. 22 Mar, 28 Mar, 29 Mar, 16 May, 7 Jul, 27 Sep. Lower Snively Spring, Snively Ranch, Bobcat Canyon, Rattlesnake Ridge/spring. *Ilythea spilota* is an uncommon inhabitant of spring habitats throughout the northwest. On Mount Rainier, it was collected only in the sedge meadow habitat (Zack 1979, 1983a). At Hanford, specimens were collected by sweeping

vegetation along the margins of several springs. The species appears to occur primarily on the substrate rather than on the vegetation.

Lytogaster gravida Loew. 29 Mar, 3 May, 16 May, 1 Jun, 21 Jun, 7 Jul, 5 Aug, 19 Aug, 15 Sep, 27 Sep, 11 Oct. Rattlesnake Spring, Lower Snively Spring, below Lower Snively Spring, Bobcat Canyon, Rattlesnake Ridge Spring. This is a geographically widespread species that can be found in most aquatic habitats with at least some partially vegetation-free areas. At Mount Rainier, it was found rarely in four of the habitat types sampled (Zack 1979, 1983a). It is most often collected close to the water's edge or in vegetation over the water. This was the case at Hanford where it was collected only along the margins of several springs.

Nostima picta picta (Fallén). 11 Apr, 24 Apr, 5 Aug, 12 Aug, 19 Aug, Lower Snively Spring, Snively Ranch, Rattlesnake Ridge/spring. This extremely handsome species is found throughout much of the Neotropical and Holarctic Regions. In Washington, it is not commonly collected but it is found in vegetation around the margins of small pools and springs.

Philygria debilis Loew. 28 Mar, 29 Mar, 19 Apr, 20 Apr, 24 Apr, 3 May, 6 May, 15 May, 16 May, 1 Jun, 13 Jun, 12 Jul, 23 Aug, 29 Aug, 27 Sep, 11 Oct. Rattlesnake Spring, Lower Snively Spring, Snively Ranch, Rattlesnake Ridge/spring, radio telescope, Rattlesnake Ridge, sand dunes. This is a common species throughout all of the northwest and much of North America. It is one of the most common shore flies found in nonaquatic habitats such as grass fields and meadows. Larvae may eventually be found in the soil of such areas, especially where moisture levels are high or consistent. I have collected adults on several golf courses in eastern Washington along the edges of fairways. At Hanford, adults were often taken sweeping flowering plants unassociated with water. At Mount Rainier, the species was abundant on the flowers of *Anaphalis margaritacea* (Zack 1979, 1983a).

Philygria nigrescens (Cresson). 15 May, 9 Jun, 10 Jun, 7 Jul, 12 Aug, 19 Aug, 29 Aug, 27 Sep. Snively Ranch, Rattlesnake Ridge/spring, radio telescope Rattlesnake Ridge. This species is found in the same habitats as *P. debilis*, but it was never as abundant as the latter species.

Pelina prospinosa Clausen. 30 Mar, 12 Jul, 20 Jul, 1 Oct. Rattlesnake Spring, Lower Snively Spring. The species is common throughout most of the western United States and south into Mexico.

The genus *Pelina* was revised by Clausen (1973) who designated several new species that, based on studies throughout Washington, occur sympatrically in many habitat types. Unfortunately, females are difficult if not impossible to identify and there may be more than one species of *Pelina* that occurs at the Hanford Site.

Subfamily Ephydrinae

Calocoenia platypelta (Cresson). 11 Oct. Rattlesnake Spring. Only one specimen of *P. platypelta* was taken by sweeping vegetation along the margin of the spring. The species is found sporadically throughout the western United States.

Ephydra packardi Wirth. 5 Aug. Rattlesnake Spring. This is a commonly encountered shore fly being found throughout much of central and western North America including British Columbia and western Mexico. *Ephydra packardi* can be very abundant along the margins of moderately alkaline ponds throughout the central basin of western North America, especially Washington. It is interesting that this species was not found at the alkaline pond habitat at the Hanford Site; in fact, no *Ephydra* spp. were found at the pond. Several other species of *Ephydra* are found throughout central Washington and could eventually be found at the Hanford Site.

Haloscatella arichaeta (Mathis). 16 May, 1 Jun, 21 Jun, 7 Jul. Rattlesnake Spring, alkaline pond. This species occurs throughout the northwestern and midwestern states. In the Pacific Northwest, it is often found in abundance along the margins of alkaline ponds and lakes. At Hanford, it was almost always taken with collections of *H. muria* (Mathis), as is common throughout central Washington. It is, however, rarely as abudnant as *H. muria*.

Haloscatella muria (Mathis). 16 May, 21 Jun, 27 Jun, 7 Jul, 5 Aug. Rattlesnake Spring, Lower Snively Spring, alkaline pond. *Haloscatella muria* is found throughout much of the United States. It is a common inhabitant of vegetation-free spring and pond margins of both fresh and alkaline waters.

Lamproscatella occidentalis Mathis. 22 Mar, 29 Mar, 11 Apr, 19 Apr, 24 Apr, 3 May, 4 May, 16 May, 1 Jun, 11 Oct. Rattlesnake Spring, Lower Snively Spring, below Lower Snively Spring, Snively Ranch, Bobcat Canyon, radio telescope, Rattlesnake Ridge. This was one of the more abundant species of shore fly taken on the Hanford Site. As are other *Lamproscatella* and *Haloscatella,* it is common around the vegetation-free margins of Washington central basin ponds and springs. However, *L. occidentalis* appears to prefer fresh or only slightly alkaline water. The species was not collected at the alkaline pond on the Hanford Site or at other alkaline ponds throughout the Washington central basin. The species occurs throughout most of western North America and western Canada.

Limnellia turneri Mathis. 22 Mar, 29 Mar, 30 Mar, 15 May, 16 May, 1 Jun, 9 Jun, 27 Sep, 11 Oct. Rattlesnake Spring, Lower Snively Spring, Bobcat Spring, Rattlesnake Ridge/spring, radio telescope, Rattlesnake Ridge, 1200 Foot Road. Although several species of *Limnellia* are found in Washington, *L. turneri* is the most commonly encountered. It was found in three different habitat types at Mount Rainier (Zack 1979, 1983a). At Hanford, it was found in both aquatic and non-aquatic habitats as well as on the flowers of chokecherry (*Prunus virginiana* L.) A few specimens of *L. turneri* were also taken while sweeping unidentified, non-flowering vegetation in areas substantially removed from water of any type.

Paracoenia bisetosa (Coquillett). 22 Mar, 20 Jun, 12 Jul. Rattlesnake Spring, Bobcat Canyon, alkaline pond. *Paracoenia bisetosa* is one of the most common inhabitants of alkaline pond margins, where larvae feed in algal mats. Aspects of life history and descriptions of immatures can be found in Zack (1983b). The species is more common in riparian areas of slightly to moderately alkaline ponds, but it is replaced by species of *Ephydra* in highly alkaline ponds. *Paracoenia bisetosa* is also found along the margins of freshwater pools and springs but never in as prodigious numbers as adjacent to alkaline pools.

Parydra aquila (Fallén). 16 May, 1 Jun, 10 Jun, 7 Jul, 12 Jul, 20 Jul. Rattlesnake Spring, Lower Snively Spring, Bobcat Canyon, Rattlesnake Ridge/spring. Species of *Parydra* are common in open riparian areas where they appear to feed primarily on diatoms. *Parydra aquila* occurs throughout the Holarctic Region and is often one of the more abundant members of the open shore, riparian shore fly community. At Mount Rainier, the species was collected in the sand shore and roadside ditch habitats (Zack 1979, 1983a). At Hanford, the species was rare, and the collection of single specimens was not unusual. This may be a result of little vegetation-free riparian area, the unstable nature of most of the Hanford spring shore lines, and a lack of substantial growth of diatoms along shorelines. The primarily open spring systems with little if any vegetational canopy may not be conducive to the diatom composition that supports *P. aquila* (but see discussion of other *Parydra* spp.).

Parydra aurata Jones. 28 Mar, 1 Jun, 7 Jul, 5 Aug. Lower Snively Spring, below Lower Snively Spring, Bobcat Canyon. *Parydra aurata* is widespread in western North America, occurring from British Columbia south to Mexico. At Hanford, the species was collected in the same habitat types as *P. aquila* but not as often. In Washington, the species is not common but appears to be fairly widespread throughout the central and eastern sections of the state. This species was very abundant around the margins of several hot springs in Harney County, Oregon, but collections from numerous other hot springs throughout Oregon and Washington do not indicate that the species is a major component of the hot spring fauna.

Parydra fossarum (Haliday). 29 Mar, 3 May, 16 May, 1 Jun, 10 Jun, 21 Jun, 7 Jul, 5 Aug, 11 Oct. Rattlesnake Spring, Lower Snively Spring, below Lower Snively Spring, Bobcat Canyon, Rattlesnake Ridge/spring. This was the most common species of *Parydra* collected at the Hanford Site. While it was not found at Mt. Rainier, it is among the most abundant and widespread of the basin species and appears to prefer warmer, open shoreline waters that are common in the central basin of Washington.

Philotelma alaskensis Cresson. New WA record. 16 May. Lower Snively Spring. Only a single specimen of *P. alaskensis* was taken at the Hanford Site while sweeping a vegetation free margin of the spring. This species has been collected from throughout central and eastern Washington, but always in small numbers. It is taken in both alkaline and fresh water situations. Additionally, new distribution records in my collection for *P.*

alaskensis include British Columbia and along the margin of the Great Salt Lake in Utah.

Scatella marinensis (Cresson). 29 Mar, 24 Apr, 16 May, 1 Jun, 5 Aug. Lower Snively Spring, Snively Ranch. This species is found throughout the western United States and southern British Columbia south to Mexico. *Scatella marinensis* was taken while sweeping emergent vegetation around each of the springs. Only one specimen was taken on each occasion. The species has been collected throughout Washington, often by sweeping emergent vegetation. I have never encountered more than three or four specimens at any collecting site.

Scatella paludum (Meigen). 3 May, 16 May, 1 Jun, 10 Jun, 21 Jun, 7 Jul, 12 Jul, 5 Aug, 16 Aug, 11 Oct. Rattlesnake Spring, Lower Snively Spring, below Lower Snively Spring, Rattlesnake Ridge/spring, Columbia River pumping station. This is one of the most common species collected at the Hanford Site and throughout the Pacific Northwest. At Hanford, the fly was found along the margins of almost all aquatic situations including the Columbia River. *Scatella paludum* was also one of the more abundant species collected at Mount Rainier, especially in the sand shore and wet woodland habitats (Zack 1979, 1983a).

Scatella stagnalis (Fallén). 22 Mar, 29 Mar, 11 Apr, 24, Apr, 3 May, 16 May, 1 Jun, 21 Jun, 7 Jul, 20 Jul, 5 Aug, 19 Aug, 29 Aug, 27 Sep, 11 Oct. Rattlesnake Spring, Lower Snively Spring, below Lower Snively Spring, Snively Ranch, Rattlesnake Ridge/spring, Columbia River pumping station, This is perhaps the most widespread and one of the most commonly encountered species of shore fly in the world. *Scatella stagnalis* occurs in all faunal regions except the New World tropics. Not only does this species have a wide geographic distribution, but it also occurs in a variety of habitat types. At Mount Rainier, it was encountered in seven of 10 habitat types sampled and was, in most of those habitats, the most abundant species (Zack 1979, 1983a). It can be taken by sweeping all riparian areas regardless of the presence of vegetation. I have not found the species around alkaline ponds or lakes.

Scatella triseta Coquillett. 22 Mar, 29 Mar, 3 May, 16 May, 1 Jun, 7 Jul. Rattlesnake Spring, Lower Snively Spring, Bobcat Canyon. A sister species of *S. marinensis*, *S. tristis* is often sympatric with the former species. At Hanford, *S. tristis* is certainly the more common species. Five or six specimens were collected for every specimen of *S. marinesis*. In collecting throughout the Pacific Northwest, I have never encountered either species in abundance. Mathis and Shewell (1978) present distributional and some natural history information on both *Scatella tristis* and *S. marinensis*.

Scatophila. The genus *Scatophila*, especially the western fauna, is in need of study. While numerous species are known to occur in the Pacific Northwest, and in Washington in particular, it is difficult to identify species based on presently available descriptions. Additionally, many new species occur in the region which serves to complicate maters. When the genus was last revised by Sturtevant and Wheeler (1954) they had few specimens from which to evaluate species differences. While they described many new species, it is sometimes difficult to place collected material into currently described taxa.

These studies suggest that certain species of *Scatophila* might be confined or better adapted to environmental conditions in the early to middle spring. Of the five species of *Scatophila* collected at Hanford, only *S. despecta* and *S. exilis* were taken after 16 May. Conditions of the spring habitats in which all *Scatophila* were collected change significantly throughout the year. These changes may affect the microorganismal fauna on which these flies feed. Zack (1983b, 1983c) found that minor habitat changes such as degree of canopy and therefore shade, could be correlated with differences in occurrence of species of *Parydra*.

Scatophila despecta (Haliday). 22 Mar, 29 Mar, 11 Apr, 24 Apr, 3 May, 16 May, 1 Jun, 10 Jun, 7 Jul, 8 Jul, 5 Aug, 12 Aug, 19 Aug, 29 Aug, 15 Sep, 27 Sep, 11 Oct. Rattlesnake Spring, Lower Snively Spring, below Lower Snively Spring, Snively Ranch, Bobcat Canyon, Rattlesnake Ridge/spring, Columbia River pumping station. One of the more abundant species of shore fly found on the Site, *S. despecta* was found to be an occasional inhabitant of the stream rocks habitat at Mount Rainier (Zack 1983a). The species has an extensive Holarctic distribution. *Scatophila despecta* from Hanford were compared with specimens from Ohio, and their genitalia appear to be identical.

One large collection of *S. despecta* was made at Lower Snively Spring on 16 May. The flies

were exceedingly abundant in the vegetation over and around this small spring. On two other occasions in the fall, at Rattlesnake Spring and Rattlesnake Ridge/spring, the flies were also the most abundant ephydrid encountered. In extensive collecting throughout the Pacific Northwest, I have never found species of *Scatophila* to be a major component of the fauna. Perhaps weather or some other environmental condition leads to the build-up of a suitable food source that allows populations to expand. All of these spring systems are subject to fluctuations, especially in the spring and fall.

Scatophila exilis Cresson. 29 Mar, 11 Apr, 16 May, 1 Jun, 10 Jun, 7 Jul, 11 Oct. Rattlesnake Spring, Lower Snively Spring, Rattlesnake Ridge/spring. *Scatophila exilis* was taken in conjunction with *S. despecta* but never in abundance. During the May 16 collection, however, six specimens were collected instead of the usual one or two. This may substantiate the hypothesis of some environmental change that favored species of *Scatophila* (see discussion of *S. despecta*).

Scatophila unicornis Czerny. New WA record. 16 May. Bobcat Canyon. Only a single specimen of *S. unicornis* was taken sweeping the margin of a vegetation choked Bobcat Spring. The species has an Holarctic distribution but was previously known only from California in the western United States.

Scatophila sp. 1. 24 Apr. Snively Ranch. One specimen of an unidentified *Scatophila* was taken by sweeping vegetation around this small spring site. The specimen appears to be very close to *S. carinata* Sturtevant and Wheeler (Sturtevant and Wheeler 1954) but does not have a black abdomen as described for that species.

Scatophila sp. 2. 22 Mar. Bobcat Canyon. One specimen of an unidentified species was taken by sweeping dense vegetation at the margin of this small spring. The specimen has the overall markings of *S. despecta* but the facial setation is markedly different.

Scatophila sp. 3. 29 Mar, 24 Apr, 16 May. Lower Snively Spring. Seven specimens of this unidentified species were taken only at Lower Snively Spring in the spring of the year. This species may have a spring or spring/fall seasonal pattern, but that would be rare for a shore fly.

Scatophila sp. 4. 29 Mar, 16 May. Lower Snively Spring, Bobcat Canyon. As with the above species, this one was taken only in the spring of the year. Five specimens of this unidentified species were collected.

Setacera aldrichi Cresson. 11 Oct. Rattlesnake Spring. This species occurs throughout much of the western United States as far south as central California. As with the following *Setacera*, only one specimen was collected at the Hanford Site from emergent vegetation at the margin of a spring.

Setacera needhami Johannsen. 11 Oct. Rattlesnake Spring. This species is commonly encountered throughout much of the more arid regions of the western United States and as far east as Nebraska. It is a common inhabitant of algal mats found around the margins of basin ponds, especially slightly alkaline ponds, throughout central Washington. Eggs are deposited into and larvae can be found feeding in algal mats. Zack (1983c) presents information on life history aspects and describes the immature stages.

Setacera pacifica (Cresson). 22 Mar. Bobcat Canyon. This is the most widespread species of *Setacera* in North America occurring throughout the western United States as far east as Michigan and along the southern border in Canada. With *S. needhami*, it can be found around the margins of many central Washington basin ponds, where it also appears to be associated primarily with algal mats. Although *S. pacifica* occurs sympatrically with *S. needhami* around the margins of alkaline ponds, I have never found it as common as *S. needhami* in these habitats.

Discussion

From the standpoint of diversity of habitats, the Hanford Site is relatively depauperate. However, the spring systems that form the aquatic ecosystems on the Site proved to have a diverse and rich fauna. Fifty-six species of shore flies in 32 genera were taken on the Hanford Site. The only comprehensive study of shore flies conducted in the Pacific Northwest was undertaken by Zack (1979, 1983a) in which I studied the fauna of Mount Rainier National Park. Of the 59 species collected at Mount Rainier only 16 were also taken at Hanford. This is probably a result of habitat types available for colonization with accompanying

differences in trophic resources. For example, Mount Rainier supported a rich fauna of *Parydra* with 11 species; only 4 species were collected at Hanford. This may be a result of available shade, water temperatures, and subsequent colonization by diatoms that appear to be a preferred food of *Parydra* spp. While not as significant, we also see differences in *Scatella*. Two widely distributed species, *S. stagnalis* and S. *paludum*, that were commonly found both at Hanford and at Mount Rainier, occupy a wide variety of habitat types, and have wide geographic distributions. Species such as *S. laxa* Cresson, *S. pentastigma* (Thomson), and *S. picea* (Walker), which were collected at Mount Rainier, represent species of boreal distribution and do not occur in the more arid regions of the Columbia Plateau and the Great Basin including the Hanford Site.

In contrast to Mount Rainier, the shore fly fauna of Hanford is consistent with that found throughout the remainder of central and eastern Washington and the Columbia Plateau in general. Examples include the rich diversity of *Lamproscatella* spp. and alkaline and warm water pond species such as *Mosillus* spp., several *Notiphila*, *Ephydra packardi*, and *Ptilomyia alkalinella*.

Of the species newly recorded for Washington in this study, I have taken most at various locales throughout central Washington. An exception is *Scatophila unicornis* which, while Holarctic in distribution, was previously known only from California and east of the Mississippi River. In extensive collecting throughout the Pacific Northwest, this is the only specimen that I have encountered. Future survey work may yield new species of shore flies and range extension records. Several other species found in central Washington and Oregon and perhaps even as far south as Utah and Nevada may eventually be found on the Hanford Site as further studies are conducted.

The Hanford Site presents us with one of the largest remaining, relatively undisturbed tracts of shrub-steppe habitat in the Pacific Northwest. The fauna and flora of the Site, including shore flies, may present us with a view of the animal and plant assemblages that more common throughout the Columbia Plateau before the advent of large-scale, especially irrigated, agriculture and urbanization.

Acknowledgements

This project was funded by The Nature Conservancy with awards from the U.S. Department of Energy, The Nature Conservancy of Washington State, and the Bullitt Foundation. The staff of Battelle Pacific Northwest Labs, especially Drs. Larry Cadwell, Lee Rogers, and Dennis Strenge were extremely helpful to the success of this project. I thank Drs. Norman E. Woodley (USDA-ARS, Systematic Entomology Lab., Washington, DC) and Wayne Mathis (Smithsonian Institution) as well as an anonymous reviewer, for their constructive remarks on the manuscript.

Literature Cited

Busacca, J. D. and B. A. Foote. 1978. Biology and immature stages of two species of *Notiphila*, with notes on other shore flies occurring in cattail marshes (Diptera: Ephydridae). Ann. Entomol. Soc. Amer. 71: 457-466.

Clausen, P. J. 1973. A revision of the Nearctic species of the genus *Pelina* (Diptera: Ephydridae). Trans. Amer. Entomol. Soc. 99: 119-156.

_____. 1977. A revision of the Nearctic, Neotropical, and Palearctic species of the genus *Ochthera*, including one Ethiopian species, and one new species from India. Trans. Amer. Entomol. Soc. 103: 451-530.

_____. 1983. The genus *Hyadina* and a new genus of Nearctic Ephydridae (Diptera). Trans. Amer. Entomol. Soc. 109: 201-228.

Deonier, D. L. 1965. Ecological observations on Iowa shore flies (Diptera: Ephydridae). Iowa Acad. Sci. 71: 496-510.

_____. 1971. A systematic and ecological study of Nearctic *Hydrellia*. Smithson. Contr. Zool. 68: 1-174.

Downs, J. L., W. H. Rickard, C. A. Brandt, L. L. Cadwell, C. E. Cushing, D. R. Geist, R. M. Mazaika, D. A. Neitzel, L. E. Rogers, M. R. Sackschewsky, and J. J. Nugent. 1993. Habitat types on the Hanford Site: Wildlife and plant species of concern. PNL-8942. Battelle-Pacific Northwest Laboratory, Richland, Washington.

Energy Research and Development Administration (ERDA). 1975. Final Environmental Statement, Waste Management Operations. ERDA-1538, Vol. 2. Energy Research Development Administration, Richland, Washington.

Foote, B. A. and W. C. Eastin. 1974. Biology and immature stages of *Discocerina obscurella* (Diptera: Ephydridae). Proc. Entomol. Soc. Wash. 76: 401-408.

Grissell, E. E. and R. S. Zack. 1996. Torymidae (Hymenoptera) new to Washington State. Proc. Entomol. Soc. Wash. 98: 827-828.

Judd, W. W. 1977. Insects associated with flowering coltsfoot (*Tussilago farfara*) at Hydepark, Middlesex County, Ontario Canada. Ont. Field Biol. 31: 43-46.

Mathis, W. N. 1979. Studies of Notiphilinae (Diptera: Ephydridae), I: Revision of the Nearctic species of *Notiphila* Fallén, excluding the *caudata* group. Smithson. Contr. Zool. 295: 1-111.

Mathis, W. N. and G. E. Shewell. 1978. Studies of Ephydrinae (Diptera: Ephydridae), I: Revisions of *Parascatella* Cresson and the *triseta* group of *Scatella* Robineau-Desvoidy. Smithson. Contr. Zool. 285: 1-44.

Mathis, W. N. and T. D. Zatwarnicki. 1995. World catalog of shore flies (Diptera: Ephydridae). Memoirs on Entomology, International. Volume 4. Associated Publishers, Gainesville, Florida. 423 pp.

Mathis, W. N., T. Zatwarnicki, and M. G. Krivosheina. 1993. Studies of Gymnomyzinae (Diptera: Ephydridae), V: A revision of the shore-fly genus *Mosillus* Latreille. Smithson. Contr. Zool. 548: 1-38.

O'Brien, C. W. and R. S. Zack. 1997. Weevils new to the state of Washington (Coleoptera: Curculionidae). Pan-Pac. Entomol. 73: 58-59.

Rickard, W. H. 1970. The distribution of ground-dwelling beetles in relation to vegetation, season, and topography in the Rattlesnake Hills, southeastern Washington. Northwest Sci. 44: 107-113

Rickard, W. H., J. H. Cline, and R. O. Gilbert. 1974. Pitfall trapping and direct counts of darkling beetles in cheatgrass communities. Northwest Sci. 48: 96-101.

Rickard, W. H. and L. E. Haverfield. 1965. A pitfall trapping survey of darkling beetles in desert steppe vegetation. Ecology 46: 873-877.

Received 28 October 1997
Accepted for publication 28 February 1998

Rogers, L. E. 1979. Shrub-inhabiting insects of the 200 area plateau, southcentral Washington. PNL-2713. Battelle-Pacific Northwest Laboratory, Richland, Washington.

Rogers, L. E., N. Woodley, J. K. Sheldon, and V. A. Uresk. 1978. Darkling beetle populations (Tenebrionidae) at the Hanford Site in southcentral Washington. PNL-2465. Battelle-Pacific Northwest Laboratory, Richland, Washington.

Sackschewsky, M. R., D. S. Landeen, J. L. Downs, W. H. Rickard, and G. I. Bird. 1992. Vascular plants of the Hanford Site. WHC-EP-0554, Westinghouse Hanford Company. Richland, Washington.

Scheiring, J. F. and B. A. Foote. 1973. Habitat distribution of the shore flies of northeastern Ohio (Diptera: Ephydridae). Ohio J. Sci. 73: 152-166.

Sheldon, J. K. and L. E. Rogers. 1978. Grasshopper food habits within a shrub-steppe community. Oecologia 32: 85-92.

Sturtevant, A. H. and M. R. Wheeler. 1954. Synopses of Nearctic Ephydridae (Diptera). Trans. Amer. Entomol. Soc. 79: 151-257.

Zack, R. S. 1979. Habitat distribution of the Ephydridae (Diptera) of Mount Rainier National Park (Washington State). Pp. 81-98 in D. L. Deonier, ed., First Symposium on the Systematics and Ecology of Ephydridae (Diptera). North American Benthological Society.

_____. 1983a. Further notes on the shore flies (Diptera: Ephydridae) of Mount Rainier National Park, Washington. Northwest Sci. 57(3): 212-223.

_____. 1983b. Biology and immature stages of *Paracoenia bisetosa* (Diptera: Ephydridae). Ann. Entomol. Soc. Amer. 76: 487-497.

_____. 1983c. Biology and immature stages of *Setacera needhami* (Diptera: Ephydridae). Proc. Entomol. Soc. Wash. 85: 10-25.

Northwest Science Forum

Northwest Science Forum provides an opportunity to articulate and discuss scientific issues in a less structured format than peer-reviewed articles. The Forum publishes short articles, opinion pieces, and letters with a focus on science and natural resource issues in the Pacific Northwest. Although the Forum is not peer-reviewed, it is edited for format and clarity. Articles should generally be less than 2000 words and contain minimal literature citations. Letters in response to articles are particularly encouraged; the original author will normally be given a chance to respond to the letter as well. There are no page charges or reprints associated with the Forum, and participants need not be members of the Northwest Scientific Association. Please send all submissions, including two hard copies and an electronic copy (any recent version of Word or WordPerfect) to the Editor.

Jennifer Sepez Aradanas, Department of Anthropology, Box 353100, University of Washington, Seattle, Washington 98195-3100

Aboriginal Whaling—Biological Diversity Meets Cultural Diversity

In 1994, the National Marine Fisheries Service (NMFS) made the long-expected announcement that the eastern Pacific population of the California gray whale (*Esrichtius robustus*) would be removed from the list of threatened and endangered species because the population had recovered to healthy levels. The gray whale is the first marine species to achieve this recovery under the Endangered Species Act. Within a year of the delisting, the Makah Indian Tribe of northwest Washington state announced their intention to resume hunting the gray whale, an important traditional resource for them.

The Makah whaling initiative has focused attention on the issue of aboriginal whaling, and on the International Whaling Commission (IWC), the group charged by multinational convention with managing the world's populations of large whales. The Tribe has always maintained that the IWC has no legal jurisdiction over their treaty right to whale, but at the behest of the United States government they agreed to engage in the international process anyway. After a year's delay, the IWC approved a 1998 subsistence quota of gray whales which included four whales for the Makah. The Tribe's initiative, and the opposition they have encountered, brings to the forefront the issue of how to manage for biological diversity in a culturally diverse world.

Makah Whaling

The Makah movement to resume hunting the gray whale is based on sound ecological principles and on the Tribe's history, culture, and beliefs. It poses no threat to the healthy status of the eastern north Pacific gray whale population and deserves the support of natural resource managers. The IWC issued a quota of 124 gray whales which will be shared by the Makah (four whales) and Russian Natives (120 whales). This quota is well below the estimated sustainable yield of 407 - 670 individuals per year (IWC 1990, 1996). The Tribe has a long history of whaling as a central cultural and subsistence practice, backed up by ample archaeological and ethnographic evidence (e.g., Swan 1868, Waterman 1920, Drucker 1951, Huelsbeck 1994). Whaling was important enough that treaty negotiators in 1855 insisted that the right to whale be specifically written into the treaty along with the more typical language concerning hunting and fishing rights. The Treaty of Neah Bay is unique in this regard.

The fact that the Tribe suspended whaling in the 1920's when the gray whale was critically endangered by Euroamerican commercial whale hunts has contributed to this species' remarkable recovery. Yet this hiatus in whaling has become an important issue for some opponents of the Makah plan. United States case law clearly establishes that the absence of practicing a treaty right in no way extinguishes that right. Furthermore, the practice of suspending whale hunts for an interval and then reviving them has been documented for other tribes in the Nuu-cha-nulth culture grouping:

> Before these men began whaling, the art had been neglected for several generations by the Ahousat. The procedure, both practical and ritual, had been kept alive in the families of the chiefs, being passed down by word of mouth (Drucker 1951:50).

Like their Ahousat relatives, Makah men today describe being taught the necessary preparatory rituals by their fathers. In addition, a whaling curriculum has been taught in the Makah reservation schools since the 1960's (Renker 1997).

Natural resource managers and others concerned with biodiversity should reward, not punish, the Makah for their contribution to gray whale recovery now that the species is off of the endangered species list and the population has increased to healthy levels. It is worth noting that the humpback whale (*Megaptera novaeangliae*), was also an important resource for the Makah (along with other cetaceans), but the Tribe has not proposed hunting it at this time because it remains endangered. This approach exemplifies responsible ecological practices and reflects the fact that the Makah have a tremendous stake in seeing that whale populations achieve and remain at healthy levels.

Aboriginal Whaling Policy

From the beginning of international whaling regulation, nations recognized that aboriginal whaling was different from commercial whaling and deserved special protection. The 1931 Convention for the Regulation of Whaling granted a blanket exemption to coastal aborigines for subsistence whale hunting. The 1946 International Convention for the Regulation of Whaling, which subsumed the 1931 Convention and chartered the IWC, contained a similar exemption for subsistence take of gray whales and a variety of right whales. This was later replaced by a system of issuing aboriginal quotas by whale stock.

A 1977 crisis over aboriginal whaling became the crucible of current IWC policy on the issue. The crisis began when the IWC revoked the aboriginal exemption for bowhead whales (*Balaenoptera mysticetus*) on the advice of scientific evidence indicating a critical level of endangerment. The bowhead ban surprised and angered many in the Alaskan Eskimo communities affected. Eskimo traditional ecological knowledge indicated that the bowhead population was significantly greater than the available scientific data on which the IWC had based its decision. Additionally, the IWC had underestimated the complex and vital significance of whaling in Eskimo culture. The Alaskan Native response to the revocation of the exemption was to declare their communities outside the jurisdiction of the IWC and NMFS, and to create the Alaskan Eskimo Whaling Commission which would allocate and manage the bowhead hunt. Intensive international negotiations and domestic conflicts followed. The United States sent armed enforcement agents into Eskimo communities (Huntington 1989), which responded by declaring that if one man went to jail the whole village would go with him (Alaska Liaison Office 1978).

The conflict was resolved when the IWC issued an aboriginal quota for bowhead whales and the United States joined with Eskimo leaders to study bowhead populations. These studies supported the validity of traditional ecological knowledge when they discovered bowhead populations significantly greater than the IWC's original estimates (Alaska Liaison Office 1978). NMFS eventually delegated its management authority to the Alaskan Eskimo Whaling Commission, and the Commission was later commended by the IWC for its management practices (IWC 1982). In 1991 the IWC concluded that aboriginal bowhead harvests have been conducted at a sustainable rate and that the stock is still recovering (IWC 1992).

Out of the bowhead crisis came a series of IWC panel reports (IWC 1982) which were to consider the issues involved in aboriginal whaling. These panels considered only data from Arctic communities targeting the bowhead whale. Thus, they examined a situation of extremely isolated communities which lacked a treaty right to whale, and were targeting an endangered species. The panels

did not consider data from indigenous communities engaged in whaling practices without IWC approval, such as in Tonga, Indonesia and the Philippines, nor did they consider communities with potential future claims on aboriginal whaling such as the Maori, Makah, and Canadian Nuucha-nulth. They did not look at any group with a treaty or written charter of aboriginal rights.

The crux of IWC aboriginal whaling policy developed in these panels was a kind of needs balancing test, valuing the subsistence needs of an aboriginal community as well as the need to preserve a given species. In this way, even an endangered species could be hunted by aboriginal whalers, but a quota would be issued for no more than would allow the population to continue recovering. For healthy whale stocks, up to 90% of the sustainable yield could be made available for subsistence take. Subsistence take was defined as whaling for the purposes of local aboriginal consumption (Donovan 1982). Within those guidelines, the number of whales issued in the quota would be based on community need, to be assessed on the basis of cultural, subsistence, and nutritional factors. These policies are generally reasonable. However, the idea of community need was left vague and broad enough as to mean one thing to whaling opponents and another to supporters.

Whale Hunting—a Proud Tradition

The issue of demonstrable need has become a focal point for some critics of Makah whaling. Congressman Jack Metcalf, for example, has been touting the idea that the Makah have not proved that whale meat is essential for their nutrition. The focus on nutritional need to the exclusion of other factors such as thousands of years of whaling history and a legally compelling treaty right is a red herring. It is an artifact of some particular studies done in reaction to the 1977 bowhead crisis and is not an appropriate international policy trajectory for decisions concerning aboriginal whaling. To allow whaling only for those groups who are suffering from some type of nutritional deficiency makes whaling into a kind of welfare program. It also assumes that whale hunting is an unseemly activity which should only be permitted under the most dire nutritional circumstances. This is not the kind of natural resource policy that will help foster diversity and understanding in a multicultural world.

For groups like the Makah, whale hunting is a proud tradition and an organizing principle of their cultural history, social relationships, and spiritual beliefs. It is not a disreputable practice to be resorted to only in the face of physical need. If the international community is to have an aboriginal whaling policy whose very purpose is to recognize the special protection warranted for traditional cultural practices, it does not bode well to base this policy on the idea that the protected practice is at heart opprobrious.

Even if degree of nutritional need were considered a legitimate evaluative condition for aboriginal whaling, this would not disqualify the Makah Tribe. Forty-nine percent of Makah households live below the federally designated poverty level, unemployment is 55 percent, and almost 60 percent of reservation housing is considered substandard (Makah Tribal Planning Department 1996; Shukovsky 1998; Renker 1997). Recently, the local food bank was serving 750 people of the town's population of almost 2,000 (Shukovsky 1998). If this does not constitute need, then Congressman Metcalf's criteria are unreasonable.

However, the dignity of Makah whaling traditions calls for a policy that would recognize their rights even if the Tribe were not demonstrably impoverished. The IWC needs to review and clarify its policy guidelines on this issue. The only appropriate assessment of nutritional need for the purposes of issuing aboriginal subsistence quota should be an assessment of how much whale the community can consume.

Conclusion

The IWC's special provisions for aboriginal whaling are commendable, although the process and guidelines need considerable fine tuning. The Makah, with the backing of the US government, were persistent and ultimately prevailed in this process. From a natural resource management perspective, going through the IWC was a responsible action on the part of the Tribe, especially when their treaty right may well have permitted them to avoid it. The issue of the Tribe's nutritional status is a diversion from legitimate criteria for deciding questions of aboriginal whaling.

Waiting until the gray whale had recovered and come off of the endangered species list was also an admirable approach. The Makah's hiatus in

whale hunting assisted in this recovery, has clear cultural precedent, and did not affect their reserved treaty right. Furthermore, natural resource managers must consider the ramifications of trying to keep once-endangered species off limits for consumptive uses even after they are recovered and delisted; the political battles to get those species that do need help on to the list will become just that much harder.

During the 1977 bowhead crisis, most environmental organizations were vehemently opposed to Eskimo whaling. Some of these same groups, such as Greenpeace USA, have not actively opposed the Makah initiative. In addition to the fact that there is no threat of stock depletion in this particular case, many in the environmental movement have come to recognize that indigenous groups can be effective allies in the struggle to preserve the world's biological capital. One group recently lamented, "It used to be simple and clear-cut. There were pro-whaling countries and organizations, and there were anti-whaling countries and organizations" (Barstow 1997). But the issue of aboriginal whaling, and of managing biodiversity in a multicultural society, demands a more complex view of the world. The debate over the Makah whaling initiative and aboriginal whaling raises many issues that natural resource managers need to consider in creating policies that also respect cultural diversity and human rights. Ultimately, policies which account for these issues will be more successful at managing resources in a complicated world.

Literature Cited

Alaska Liaison Office. 1978. Hunger Knows No Law. Alaska Liaison Office, Anchorage, Alaska.

Barstow, R. 1997. Turmoil at the IWC: A test of wills. Whales Alive! VI(4).

Donovan, G.P. 1982. The International Whaling Commission and aboriginal subsistence whaling: April 1979 to July 1981. Reports of the International Whaling Commission Special Issue 4:79-86.

Drucker, P. 1951. The Northern and Central Nootkan Tribes. Smithsonian Institution Bureau of American Ethnology Bulletin 144. United States Government Printing Office, Washington DC.

Huelsbeck, D.R. 1994. The utilization of whales at Ozette. In S.R. Samuels (ed.) Ozette Archaeological Research Reports, vol. II, Fauna. Washington State University Department of Anthropology, Pullman, WA. Pp. 265-303.

Huntington, H.P. 1989. The Alaska Eskimo Whaling Commission: Effective Local Management of a Subsistence Resource. Scott Polar Research Institute, University of Cambridge, Cambridge.

International Whaling Commission. 1982. Aboriginal/subsistence whaling (with special reference to the Alaska and Greenland fisheries). Reports of the International Whaling Commission Special Issue 4:1-50.

International Whaling Commission. 1990. Report of the Special Meeting of the Scientific Committee on the Assessment of Gray Whales. International Whaling Commission.

International Whaling Commission. 1992. Report of the Scientific Committee. Reports of the International Whaling Commission 42.

International Whaling Commission. 1996. Draft Report of the Scientific Committee. International Whaling Commission IWC/48/4.

Makah Tribal Planning Department. 1996. Makah Marina Project—United States Department of Housing and Urban Development, Indian Community Development Block Grant Application. Makah Tribal Council. Grant Application on file with Makah Housing Authority, Neah Bay, Washington.

Renker, A. 1997. Whale hunting and the Makah Tribe: a needs statement. Appendix 8.2 in Environmental Assessment of the Makah Tribe's Harvest of up to Five Gray Whales per year for Aboriginal Subsistence Use. United States Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Office of Protected Resources, Silver Spring, MD.

Shukovsky, Paul. 1998. Bleak days for Neah Bay's Makah: Tribe turns to new ventures for economic recovery. Seattle Post-Intelligencer. March 30, 1998.

Swan, J.G. 1868. The Indians of Cape Flattery, at the Entrance to the Strait of Fuca, Washington Territory. Smithsonian Contributions to Knowledge No. 220. Smithsonian Institution, Philadelphia.

Waterman, T.T. 1920. The whaling equipment of the Makah Indians. University of Washington Publications in Political and Social Science 1:1-67.

Book Reviews

The Science of Conservation Planning—Habitat Conservation Under the Endangered Species Act

Reed F. Noss, Michael A. O'Connell, and Dennis D. Murphy, Island Press ($40 cloth, $25 paper)

The Endangered Species Act (ESA) of 1973 was instituted to counteract the alarming rate of plant and animal extinction. Despite the ESA mandate to conserve the ecosystems on which threatened and endangered species depend, most efforts at species recovery have used a species by species, rather than a broad-scale habitat-based approach. Habitat-based conservation planning emerged under the crisis atmosphere of excessive human population growth and rapid economic development. Regions such as southern California and Florida, where high species endemism and biodiversity seem at odds with economic growth, have become test cases for habitat-based conservation planning. The purpose of the book is to encourage the use of habitat-based conservation planning as a tool for biodiversity conservation. In seven chapters, the authors effectively demonstrate that proactive habitat-based conservation planning is more efficient, cost-effective, and scientifically defensible than single-species approaches.

Habitat-based conservation plans are defined as "conservation plans that takes into consideration the overlapping habitat requirements of multiple species within the context of a functional community or ecosystem." The book defines this and other key terms such as habitat, community, ecosystem, and metapopulation in the "Notes from the Authors" section. This approach may seem sophomoric to some readers, but it is useful and appropriate given the potentially diverse audience. The book is appropriate for a multiple audience, from academics to business advocates. It is challenging to write to such disparate interests, but the book both reviews the basic concepts of conservation biology, and develops specific recommendations for habitat-based conservation planning.

Chapters 1 and 2 review the principles and history of conservation biology. The authors justifiably criticize the single species approach to conservation planning. Even under the protection of the ESA, more species are declining than improving, and human induced habitat loss and degradation are the chief cause of this decline. Chapter 2 provides an excellent history of conservation planning in the United States, and details the role of the ESA in the planning process. Specifically, section 7, consultation on public lands, and the Habitat Conservation Plan process on private lands are reviewed in detail. The authors indicate that these ESA approaches have largely been ineffective because of their single-species and small-area focus. As a result, multi-species and ecosystem planning are suggested as an alternative, and California's Natural Communities Conservation Planning program is cited as an example.

Chapter 3 addresses criticisms of habitat-based conservation plans. Many environmentalists criticize the habitat-based conservation plan as a way for development interests to undermine the ESA. Interestingly, the authors note that the ESA does not address many of the principal factors influencing the survival of a species, including habitat fragmentation, protection of suitable but unoccupied habitats, and control of exotic species. Habitat-based conservation planning offers a proactive approach to avoid habitat destruction that would lead to listing of species under the ESA.

Successful habitat-based conservation planning is grounded in philosophical principles. Given the rate of species extinction, it is unjustifiable to try to learn everything about each species. Instead, the authors suggest that biology must provide a foundation for an understanding of ecosystem response to human activities. Chapter 4 reviews these principles, as well as components of reserve design, and principles of community and ecosystem conservation. Chapter 5 expands upon these principles as a means of assessing the adequacy of conservation plans. The authors propose the optimal approach to improving conservation planning is to use and learn from cases studies as demonstration projects for future

conservation efforts. The appendices of Chapter 5 provide detailed case studies of habitat-based conservation plans, including examples from Brevard County, Florida, and the Coachella Valley and Orange County, California. These case studies set the stage for chapter 6, "A Framework and Guidelines for Habitat Conservation." This chapter will be particularly useful to researchers and managers charged with the responsibility of implementing conservation plans. The scientific methods to evaluate alternative plans, population viability assessments, sustenance of ecological and evolutionary processes, and adaptive management issues are reviewed extensively.

Chapter 7 concludes with specific recommendations to all parties involved in conservation planning. These recommendations are painfully honest. For example, developers are advised that their "wealth and political influence" may not carry the day in the conservation planning process, and environmentalists are admonished that "like it or not this process is here to stay." I found this directness refreshing. As Noss notes in the Preface, "conservation planning is not for the faint of heart."

The science of conservation biology has made great advances in the past two decades, but policy and planning have lagged far behind scientific understanding. This book will help bring habitat-based conservation planning up to date. The organization of the book allows the reader to quickly review basic principles, or explore specific topics or case studies in more detail, making the book appropriate for the citizen activist, researcher, manager, or businessperson. I urge all those interested in conservation biology to add this book to their collection.

— Eric K. Cole
Forest Science Department
Oregon State University
20 Forestry Sciences Lab
Corvallis, OR 97331-7501

Northwest Birds in Winter
Alan Contreras, 1997, Oregon State University Press ($17.95)

Flitting Dark-eyed Juncos rise to a winter perch on the cover of this new addition to northwest ornithology. In *Northwest Birds in Winter,* Alan Contreras breaks with tradition in North American bird books and spends nearly 290 pages presenting a synthesis of the known distribution and relative abundance of birds in northwestern North America in *winter.* Few authors have taken such a pure approach, focusing on winter status and ignoring a discussion of the breeding season.

Contreras was uniquely qualified to carry out such a work. He has lived in the area since boyhood, birded the area since 1967 and served as Oregon-Washington Christmas Bird Count (CBC) editor in the late 1980s and early 1990s. Contreras has participated in "countless Christmas Bird Counts," and has written numerous how-to articles, summaries, and reviews of Oregon Christmas Bird Counts, primarily published in *Oregon Birds* and *Western Birds.* It is clear that winter birds and birding have stolen the heart of this northwest field ornithologist.

The region covered in this book includes the U.S. states of Idaho, Oregon, and Washington, and the southern part of the Canadian province of British Columbia. Contreras roughly defines winter for his purposes as December, January, and February, recognizing that for some species this period can actually include some migration.

The purpose of the book is to introduce birders and naturalists to the winter avifauna of the region and compile in one reference much information that is otherwise scattered throughout a myriad of obscure publications, CBC forms, and field notes. There is a brief introductory section, but most of the book is devoted to short accounts of approximately 420 species of birds known to have occurred in the region in winter.

In the introductory pages Contreras outlines the purpose and scope of the book, summarizes the winter birding experience, briefly describes some of the best locations to observe diverse groups or interesting species of birds, and provides some guidance for interpreting maps and various terms used in the text. For more detail on birding sites, an annotated list is provided of 18 different references for bird-finding in the region by state or province.

The species accounts are short, to the point, and easy to read. Contreras broadly descries relative abundances and distributions of each species. He does not delve into detailed habitat associations or management considerations, but does describe general habitat types utilized by each species. Numbers of birds seen in specific locations and maximum numbers reported are occasionally listed, giving the reader a more exact sense of the abundance of some species.

An approximately 2- x 2-inch distribution map is provided for the 256 or so regularly-occurring species. Two shades are used to indicate regions of more-frequent or less-frequent occurrence. The maps are fairly coarse, but nonetheless they give the reader a general idea of the winter distribution of the regularly-occurring species. I found most ranges and general abundances to be accurately portrayed at a coarse scale. One area that seemed to give the author some trouble was the Cascade Range. Some species which are for the most part absent in the Cascades in winter are shown as present (e.g., European Starling, American Crow, Mourning Dove, Golden-crowned Sparrow, and White-crowned Sparrow), while others are correctly portrayed as (mostly) absent in winter (e.g., Northern Shrike, Rock Dove, American Goldfinch, House Sparrow, and House Finch). Similarly, Mallard and Great Blue Heron are shown as wintering in the Cascades, which they do in small numbers, while Common Goldeneye, Barrow's Goldeneye, Common Merganser, and Hooded Merganser are shown as absent, when in fact the latter group is more often found in the Cascades in winter than the former group. A few mapping bloopers are present, such as the northwest Oregon distribution of Merlin, which was intended to show the bird being absent in the Coast Range rather than the west edge of the Willamette Valley.

To my knowledge, winter range maps at this level of detail for northwest birds have previously been published only in the *Atlas of Oregon Wildlife* (Csuti et al. 1997, Appendix III, also prepared by Contreras), and in *Birds of British Columbia* (Campbell et al. 1990, in which CBC circles were used to represent the species' ranges).

For approximately 184 species, a summary of Christmas Bird Count data is presented for each political entity in the region (i.e., British Columbia, Washington, Oregon, Idaho), as well as for the continent as a whole. Statistics given are for percent annual trend, number of CBC circles used to generate the information shown, and an average number of birds observed per 100 person hours. No indication is given of the significance levels of any trends, and no measure of variation is given for the birds-per-100-person-hours figures. However, in the appendix the reader is referred to a CBC web site maintained by the U.S. Biological Service that provides additional detail.

The pen-and-ink sketches and paintings (reproduced in black-and-white) of Eugene, Oregon, artist Ramiel Papish are superb, and bring to life about 30 pages of the book. This book also contains one of the most extensive published collections of photographs (in black and white) of rare winter birds in the Pacific Northwest. While some of the photographs are of mediocre quality, most birders appreciate the difficulty of obtaining photographs of many of these birds, and will consider the photos valuable documentation of birds' occurrence.

An altogether different feel for Northwest birds emerges from this book. Most bird books emphasize breeding birds, and portray the independent behavior exhibited by most paired birds (especially songbirds). However, in winter, the majority of birds forage in groups, fly in flocks, and roost communally. The winter is a time of gathering for most northwest birds.

Birders, field-ornithologists, and biologists will find this an enjoyable guide which stimulates an interest to further explore northwest birds in winter.

— Matthew G. Hunter
Department of Forest Science
Oregon State University
Corvallis, OR 97331

Literature Cited

Campbell, R., N. Dawe, J. Cooper, G. Kaiser, M. McNall, and I. McT. Cowan. 1990. Birds of British Columbia. Volumes 1 and 2. Royal British Columbia Museum.

Csuti, B., A. J. Kimerling, T. A. O'Neil, M. M. Shaughnessy, E. P. Gaines, and M. M. P. Huso. 1997. Atlas of Oregon wildlife: distribution, habitat, and natural history. Oregon State University Press, Corvallis.

Atlas of Oregon Wildlife - Distribution, Habitat, and Natural History

Blair Csuti, A. Jon Kimerling, Thomas A. O'Neil, Margaret M. Shaughnessy, Eleanor P. Gaines, and Manuela M. P. Huso, 1997, Oregon State University Press ($39.95)

Knowing the distribution of species is fundamental to most aspects of ecology and natural resource management. Although a number of guides presenting information on the distribution and natural history of different vertebrate groups have recently been published, this work is the first to provide a comprehensive look at the natural history and distribution of all terrestrial vertebrates that breed in Oregon.

The book begins with a brief introduction describing the approach used to construct the maps and a description of the wildlife habitats of Oregon. The core of the book (443 pages) consists of maps depicting breeding distributions and brief summaries of the natural history for the 441 species of amphibians, reptiles, birds, and mammals included in the book. The work concludes with a glossary, list of references, appendices with checklists of terrestrial breeding species and wintering bird species, distribution maps for wintering bird species, and an index. A map of wildlife habitats for the state is included in a pocket on the back cover.

The heart of the book is divided into four major sections corresponding to the four Classes of terrestrial vertebrates; entries are arranged taxonomically within these sections. There is no table of contents at the front of the book or in the front of chapters to help identify exact locations of entries. As a result, the reader must resort to turning to the index or (as I generally do) to flipping through a general area of the book to find specific entries. Having a logical order to the entries (such as alphabetical within family or genus) or a table of contents at the beginning of each section would have facilitated use of the book.

The primary interest in the book will undoubtedly be the range maps provided; the approach used to construct the maps is novel. The foundation for the maps is a matrix of 441 equal-area hexagons that overlay the state. The hexagons form the spatial accounting system for individual records for locations of each species. General distributions of species were mapped onto these hexagons based on information gathered from museum specimens, published literature, expert opinion, and other sources. A map of the distribution of habitat types was overlaid on this. The habitat types were generated from the locations of 133 vegetation cover types grouped according to similarities in composition of vertebrate communities; vegetation types with similar vertebrate communities were lumped together into a single habitat type. Species distributions were then refined based on habitat associations, and a final map constructed based on the geographic overlay of suitable habitat types within the general species distribution. The maps were reviewed by 45 highly qualified people, many of whom are leaders in their fields and have intimate knowledge of the natural history and distribution of particular taxa.

The maps are presented as light gray relief maps with distributions of species shaded blue. The result is a high quality and aesthetically pleasing presentation. As species distribution maps were based on mosaics of habitats, the resulting maps show animal distributions with uneven edges and, frequently, with patches of unoccupied habitat within the overall distribution. The maps derived using this approach leave the impression of distributions that are "patchy." As actual species distributions are typically patchy, the general visual impression of the maps reflects reality. However, this approach also leaves one with a false impression of precision - that the mapped location of habitat and non-habitat corresponds precisely to actual distributions of species. For example, the map of the Douglas squirrel (p. 377) depicts the species as being absent from a number of relatively small patches in the coastal and Cascade mountains corresponding to "early shrub-tree" habitat. Over relatively short time frames, many of the areas mapped as early-tree shrub habitat will develop into suitable habitat as areas are reforested, whereas other patches will enter this habitat type as areas are disturbed following logging or fire. Consequently, at best these maps represent a snapshot in time for this and similar species. The map also indicates that the entire Willamette Valley, with the exception of urban areas corresponding to Eugene, is suitable habitat for Douglas squirrels, though in reality much of the valley does not provide suitable habitat for

this species. Although the authors warn that maps created using this approach result in making "unavoidable generalizations about the distributions of species," the striking visual imagery resulting from the maps makes it difficult to avoid interpreting the distributions as precise.

The approach used to construct the maps is based several assumptions. Among these are: 1) habitat types based on vertebrate community composition describe key habitat components influencing the distribution of individual species; 2) habitat types are accurately mapped; 3) presence of a species is a function of the availability of suitable habitat, and 4) species can be accurately assigned to habitat types. For many species these assumptions are reasonable, and the distribution of these species can be mapped reasonably well using this approach. This method is likely to overestimate distributions for species that are strongly associated with special features or specific uncommon habitat components occurring at the microsite scale. The authors allude to this problem in the preface to the book, indicating a major limitation being the "inability to map important but small habitat features." At the other end of the spectrum of spatial scales, the approach used to generate the maps may also overestimate distributions of species that are strongly influenced by landscape structure. Although this may be problematic for a few species, recent research suggests that distribution of many species is more strongly influenced by landscape composition (i.e. habitat type) than by landscape pattern, and so this is not likely to be an issue for most species. A potentially greater problem relates to how well *species* distributions can be predicted from distributions of habitat types constructed based on vertebrate *community* composition. It is increasingly accepted that compositions of temperate communities lack cohesion and are artifacts of forces acting on individual species. As a consequence, using community-based parameters to identify species distributions is likely to result in inaccuracies for some species.

The narrative information for each species account is generally accurate and complements the maps nicely. The brevity of the narrative information (required by constraints of space) may be frustrating to some, and at times this necessitated broad generalizations for a species. However, for those wishing to go into greater depth, the handful of references presented with the narratives provides a gateway to more in-depth information. Each entry is illustrated with a depiction of the species. The quality of the drawings is generally high, although the quality of drawings for mammals is uneven and presented using several different drawing styles.

Despite some shortcomings, by perusing the resulting maps of species distributions, it is almost impossible not to learn something new about the biology of vertebrates in Oregon - I certainly did. Overall, this atlas is a valuable resource for managers, biologists, and students of nature. A copy of this book should adorn the bookshelf of anyone interested in the biology or natural history of vertebrates in Oregon.

— John P. Hayes
Department of Forest Science
Forestry Sciences Lab
Oregon State University
Corvallis, OR 97331-7501

Sea-Run Cutthroat Trout: Biology, Management, and Future Conservation

Edited by: James D. Hall, Peter A. Bisson, Robert E. Gresswell, Oregon Chapter of the American Fisheries Society ($20.00)

Without a doubt the least researched and perhaps most complex salmon of the Pacific Coast would have to be the cutthroat trout (*Oncorhynchus clarki clarki*). I gained these, and many other insights recently, when I reviewed the 183 page proceedings of the Sea-Run Cutthroat Trout Symposium, Edited by: Drs. James D. Hall, Peter A. Bisson, and Robert E. Gresswell (1997). On October 12-14, 1995 a well attended conference devoted to sea-run cutthroat trout was held at Reedsport, Oregon. Due to the efforts of these editors, along with a distinguished list of contributors, we now have a professionally prepared reference on sea-run cutthroat to enjoy and learn from.

The enthusiastic welcome of this conference by the community of Reedsport, Oregon is highly evident in the Introduction by Dr. John Crocker, Conservation Director, Lower Umpqua Flycasters. As was pointed out by Dr. Hall in the Preface: Dr. Crocker's exceptional contribution of time and effort in large measure brought about the success of this effort. Throughout his introduction Dr. Crocker hands out credits to others, and stresses the need for knowledge on all facets of the life history and ecology of sea-run cutthroat trout. As I read his introduction I couldn't help being struck with his sincere desire for knowledge about the sea-run cutthroat, something I find quite refreshing.

The symposium presentations were carefully organized into four major sections: (1) biology, (2) status of the stocks along the Pacific Coast, (3) a case study, and (4) future management and conservation. There were also a number of contributed papers and a poster session. The 1993 petition for threatened or endangered status of the Umpqua River sea-run cutthroat trout (subsequently listed as endangered in August 1996), made it the logical choice for the case study subject.

Chapter one on biology establishes the complexity of the life history and ecology of the Pacific Coast sea-run cutthroat, in both aquatic and marine waters. Chapter two gives a coastwide status review of sea-run cutthroat from California to Alaska, pointing out the lack of good data bases on this species, and the indication of highly variable populations throughout their range. This chapter also paints a picture of highly diminished runs in the southern portions of the range, and variable to increasing populations in the north. Chapter three covers the biological status and low runs of sea-run cutthroat in the Umpqua River basin, and offers strategies for restoration. Chapter four gives a variety of recovery strategies, with both professional and nonprofessional perspectives, for sea-run cutthroat. Chapters five and six provide a wide spectrum of reports on studies on cutthroat trout from California to Alaska.

This compilation of work on sea-run cutthroat provides a firm reference for scientists and sportsmen alike to access for a collection of the existing knowledge on this species. It not only compiles the most recent information on sea-run cutthroat, it is also organized in a logical and very readable manner. After finishing the many fine articles, I came away with a far better appreciation for the plight of the sea-run cutthroat, it's life history, vulnerabilities, and status. I am left, however, with a feeling of sadness; because cutthroat also find themselves in the unenviable condition of suffering from widespread habitat loss and over fishing, a legacy far too often played out in the presence of European man.

The proceedings establish the variable status of sea-run cutthroat along the Pacific Coast, a difficult task considering the scarcity of information on this species. As I read the chapters on stock status I couldn't help but reflect on man's impact on the Pacific salmon in general, starting in California and progressing northward. One can't help but notice the apparent inverse relationship between more people and less fish. More people seems to always bring more habitat degradation, more hatcheries, more dams, and more over fishing, the impacts of which have cumulatively contributed to the detriment of many salmon populations.

The proceedings has taught me that more data doesn't necessarily mean better management. Even in the few cases where we have good information on the causes and effects of habitat degradation on sea-run cutthroat trout, we still haven't fully used that knowledge. For example, this report points out the documented vulnerabilities of

cutthroat to logging practices in the Alsea Watershed Study, yet logging has continued, often unabated. This lack of attention to research data is demonstrated in the North Umpqua River case study information, where returning wild sea-run cutthroat counts over Winchester Dam date back to the early 1940s. These counts clearly trace the demise of the North Umpqua sea-run cutthroat during the mid 1950s, yet the answer at that time was to plant hatchery fish, and continue logging. After the hatchery fish plants were discontinued in the mid 1970s, the underlying lack of wild sea-run cutthroat again became evident. Even in light of this clear data set, logging continued at a very high rate in the Umpqua National Forest clear into the middle 1990s.

It must be said that much of what we know about sea-run cutthroat has been collected coincidentally with it's more widely researched relatives, and this has compromised our ability to gain a clear understanding of this species. The proceedings point out that to recover lost populations of sea-run cutthroat will take a major effort by all parties, including: loggers, farmers, city planners, fishermen, and even policy makers. Much emphasis is placed on the need to pay greater attention to the overall sea-run cutthroat ecosystem, if we really want to recover these populations. It points out that protection and conservation of habitat, reliable implementation guidelines, and comprehensive monitoring programs are essential. These ideas provide the reader with a good sense of the difficult problems that sea-run cutthroat face, but also gives hope that working together under an ecosystem based approach may offer a path to success.

If I had one criticism of this conference, I guess it would be the noticeable lack of attention paid to the interspecies effects of other salmon population declines on sea-run cutthroat abundance. For example, I would have appreciated an examination of how closely North Umpqua River sea-run cutthroat have followed the declines of other coastal salmon species, such as coho and chinook salmon. The predatory interactions and perhaps dependence of sea-run cutthroat on other salmon as a food source has been noted in the literature, yet little attention is given to this aspect of sea-run cutthroat life history.

If there is, eventually, another symposium on sea-run cutthroat trout, it will be hard to improve on this product. It is as good a mixture of both professional and nonprofessional collaboration as one could hope for. A collaboration that I feel sure will be a critical element in the eventual realization of the goals that Dr. Crocker pointed out in the introduction of the conference.

In the future I know that even more information will come forward and build on the firm foundation that this publication has established. Below I have listed some possible topics that a future conference on sea-run cutthroat trout might address. Some of the new research, alluded to in the proceedings, will no doubt vastly expand our understanding of the complexity of genetic diversity of sea-run cutthroat stocks, particularly between tributaries of a single river basin.

Other research may soon give us a better understanding of the interrelationship of the headwater nonanadromous forms of cutthroat, and the freshwater migratory forms that live in sympatry with sea-run cutthroat. I would hope to see a paper that investigates how well cutthroat have fared in light of declining salmon runs and the subsequent loss of carcass nutrient to spawning streams. Also, it would be helpful to see more emphasis on the impacts of sport and commercial fisheries on sea-run cutthroat populations, in both fresh and marine waters.

This sea-run cutthroat trout proceedings is an outstanding reference, and is an especially good example of how fish professionals and nonprofessionals can work together to expand our knowledge base. I recommend it as an important reference for all fish biologists and sportsmen, alike. Dr. Hall can rest assured that the proceedings will excite enthusiasm in many future generations of biologists, anglers, and conservationists, and I echo the hope that Dr. Hall expressed: that the future of this remarkable fish will be secure.

—Jeff Cederholm
Department of Natural Resources
Resource Planning & Asset Management
PO Box 47014
Olympia, WA 98504-7014

Eco Homo: How the Human Being Emerged from the Cataclysmic History of the Earth
Noel T. Boaz, New York: Basic Books, ($25.00)

Nearly everyone is familiar with global warming, El Niño, and holes in the ozone layer. Today there is great interest, and concern, about climate change and its implication for the future of our planet and for our health and quality of life. A less widely popular topic, but one that is rapidly growing, is how climate change in ancient times may have influenced animal life generally, and the evolutionary development of our human and pre-human ancestors, in particular. *Eco Homo* is the most recent addition to a group of popular science books that examine the impact of climate change and ecological instability on the physical adaptations, geographic distribution, and evolutionary transformation of our early human ancestors.

The book is organized around nine scientific hypotheses concerning evolutionary events leading up to the origin of modern humans. A summary of these nine hypotheses provides a good measure of the diverse issues Boaz discusses. Hypothesis One "concerns the split of our lineage from that of our largest cousin, the gorilla." The idea that evolutionary divergence of ancient chimps and human ancestors occurred because geological upheaval created the Western Rift Valley system that isolated these hominoid groups from one another comprises Hypothesis Two. The third hypothesis takes an unusually broad perspective of hominid origins since it goes beyond South and East Africa, the centers of early hominid fossil discovery. It adopts a pan-African perspective and proposes that climate change in the Sahara— the expansion of deserts — may have been a contributing factor in the splitting of the chimp and human lineages.

Major evolutionary changes in the savannah / grassland dwelling australopithecines are related to a progressively more variable climate in Hypothesis Four. The global impact of such distant climate change as the formation of polar ice caps and increasingly severe climatic fluctuations in the tropics is related to the origins of the first members of the genus *Homo* in the fifth hypothesis. The development of a 'paleoclimatic pump' model for repeated latitudinal habitat shifts is proposed in Hypothesis Six, to account for the dispersal of *Homo erectus* from the Africa into Eurasia. An ecological argument for the expansion of modern humans into Europe between 35 and 32 thousand years ago and extinction of Neandertals constitutes Hypothesis Seven. And finally, the developmental origin culture 'as we know it' is explained in Hypothesis Eight, as a consequence of the severe environmental fluctuations of the late Pleistocene.

The book is well written and carefully edited making it an enjoyable reading experience. Each of the hypotheses is framed in historical or theoretical context, and consideration is given to the nature of evidence required to confirm or reject each one. This gives the reader a more complete understanding of how the scientific method is applied to paleontological hypotheses, and how advances are made in the field of paleoanthropology. The diverse foundations and methods of paleoecological reconstruction are presented clearly and concisely making it easy to understand how ancient habitats and ecosystems are recreated by interdisciplinary teams that include paleoecologists and paleoanthropologists. In general, I found the discussion of Hypotheses One through Three more convincing and credible because they are based on firmer theoretical and scientific foundations than later hypotheses. Beginning with Hypothesis Four, Boaz tends to rely more heavily on greater doses of speculation, modern behavioral analogy, and 'best guesses'.

The discussion of australopithecine lifeways, for example, relies too heavily on behavioral analogy with modern Africans, and even modern fossil collectors! We learn that, "Modern Africans who live in the savannah can do quite well without physical exertion in the middle of the day." (p. 124). While this may be true, it does not constitute proof that early hominids could also thrive in the absence of mid-day activity. In fact this assertion contradicts the diurnal hunting hominid hypothesis which advocates just the opposite. Furthermore, we learn that like modern Africans our early hominid ancestors, "...would have found a nice shady acacia tree to sit under at noontime" (p. 124), and "...may have dug ephemeral sandy stream beds for water, eaten water-laden succulent plants growing in the savannah, and even carried water in some sort of container." In my

opinion, valid paleoecological reconstruction must be based upon tangible evidence from the past. Evidence from the fossil remains of plants and animals associated with early hominids and from the geo-ecological context of burial are relevant bases for paleoecological inference— not the behavior of modern African *Homo sapiens.* I thought the practice of assessing early hominid lifestyles on the basis of observed behavior of modern humans, or apes, had been abandoned a decade ago in favor of empirical evidence. Basing a reconstruction of australopithecine lifeways, even partially, on modern behavioral analogy is prone to error, inconsistent with prevailing paleoecologial methodology, and should be vigorously and assiduously avoided. It takes great skill to write well enough to retain a diverse audience and simultaneously to portray scientific concepts and methods accurately.

Another example of naive interpretation is Boaz' contention that skull form in *Homo erectus* represents a protective adaptation to "...external blows, from the front and back as well as from above."(p. 177). Boaz offers no alternative hypotheses for *Homo erectus*' cranial features, though biomechanical forces involved in using the teeth and jaws as a third hand or vise-grip make a compelling and well integrated explanation (Wolpoff, 1980). Odd statements arise throughout the book that make you wonder, in the absence of explanation or reference to other researcher's ideas, how did the author arrive at this conclusion? For example, we are never informed how Boaz came to the conclusion that *Homo erectus* "...probably had the mental abilities of a an average five-year-old." (p. 177).

A systematic fault, but perhaps one to be overlooked in a 'popular science' book, is apparent biased attention to the research of others, and the incomplete nature of citations and references to paleoecological and evolutionary research. The research of J. Arnold Shotwell, a University of Oregon paleontologist who developed innovative and widely acclaimed methods of paleoecological reconstruction in the 1950s and1960s is discussed, but his work is not cited in the bibliography. Others paleoanthropologists who have advanced ideas in parallel or in opposition to Boaz are either not mentioned, not discussed, or not cited. The likes of Phil Rightmire, Tim White, Milford Wolpoff, and Bernard Wood come to mind, though there are numerous others.

Having taught an advanced seminar in paleoecology and human evolution for many years, I found it easy to distinguish Boaz' speculation from the hard factual evidence he uses to support one hypothesis or another. However, I suspect that neophytes to these intriguing issues of ancient ecologies and human origins may equally easily confuse fact with fiction since the author does not always clearly differentiate the two.

Despite its shortcomings, this book has much in the way of new and original ideas to offer the student of human origins and evolution. Its primary value lies in emphasizing that human origins and the evolution of human adaptations occurred within a set of complex ecological interactions between hominids and their environment. Those who wish to pursue the topic of ecological instability and its impact on human evolution further, and to gain insights from other leaders in the field, should read the books by Potts (1996) and Stanley (1996) cited below. A sobering final thought for reflection. Climatic change often stimulates the creative fluorescence of many new plant and animal species; it also brings about the extinction of many others. Will our highly developed cultural adaptations permit modern humans to embark on a new evolutionary trajectory, less directly influenced, or independent of climatic oscillations?

— John R, Lukacs, Ph.D.
Department of Anthropology
University of Oregon
Eugene, OR 97403-1218

References

Potts, Rick 1996. Humanity's Descent: The Consequences of Ecological Instability. New York: William Morrow & Co.

Stanley, Steven M. 1996. Children of the Ice Age: How a Global Catastrophe Allowed Humansto Evolve. New York: Crown Publishers

Wolpoff, MH 1980. Paleoanthropology. New York: Alfred A. Knopf.

Errata

A technical flaw in word choice was detected by A. B. Carey (pers. comm.) in the abstract of my article entitled "Breeding Bird Abundance and Habitat Relationships on a Private Industrial Forest in the Western Washington Cascades" which was published in Volume 71, No. 3, 1997 of *Northwest Science.*

In the Discussion, I stated that my study showed equal or greater species richness than other breeding bird studies on federal lands in the southern Washington Cascades (which was a true statement at the time of writing). Subsequently, when I wrote the abstract, I tried to keep it short by substituting "Pacific Northwest" for "western Washington Cascades" which was already presented in the title, visible just above. Unfortunately, this attempt at brevity resulted in a spurious statement, for there were several studies from Oregon that had higher species richness on federal lands (see Carey 1991; Gilbert and Allwine 1991), a fact that I was well aware of while writing the Discussion, but had forgotten while composing the Abstract (the last task of the writing process).

Carey (pers. comm.) also commented that such a comparison of species richness could be misleading because of the widely differing methods and experimental designs used by each investigator. For example, Carey (pers. comm.) related that the studies by Manuwal (Manuwal and Huff 1987; Manuwal 1991) included only birds observed within 75 m of points excluding birds flying overhead (except for Vaux's swifts) and only birds detected more than 2 times within a stand (i.e., raptors and waterfowl were not included). I generally agree that the comparisons were somewhat strained by these factors, but the important point was to derive a *rough* idea of how industrial forests compare among other forest management types previously reported for this region. These comparisons were not made to portend that commercial timber harvesting on private lands was better conservation for breeding birds than management practices used on Forest Service lands. As I fully admitted in the Discussion of the paper, a higher number of point counts and "inclusion of wetlands and clearcuts...helped to increase species richness for the tree farm." In terms of conservation of breeding birds in late-successional forest, my results generated the same dogma as others, that retention of mature coniferous forest (a result of sustainable forestry and new forestry) is vital to the future survival of many species within breeding bird communities of the Pacific Northwest.

—Thomas Bosakowski
Beak Consultants Inc.
12931 NE 126th Place
Kirkland, WA 98034

References

Carey, A. B., M. M. Hardt, S. P. Horton and B. L. Biswell. 1991. Spring bird communities in the Oregon Coast Range. Pages 123-144 *In:* Ruggiero, L. F., K. B. Aubry, A. B. Carey, and M. H. Huff, tech. coords. Wildlife and vegetation of unmanaged Douglas-fir forests. USDA Forest Service Gen. Tech. Rep. PNW-GTR-285. 533 pp.

Gilbert, F. F. and R. Allwine. 1991a. Spring bird communities in the Oregon Cascade Range. Pages 145-160 *In:* Ruggiero, L. F., K. B. Aubry, A. B. Carey, and M. H. Huff, tech. coords. Wildlife and vegetation of unmanaged Douglas-fir forests. USDA Forest Service Gen. Tech. Rep. PNW-GTR-285. 533 pp.

Manuwal, D. A. 1991. Spring bird communities in the southern Washington Cascade Range. *In:* L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, tech. coords. 1991. Wildlife and vegetation of unmanaged Douglas-fir forests. USDA Forest Service Gen. Tech. Rep. PNW-GTR-285. Pp. 161-176.

Manuwal, D A. and M. H. Huff. 1987. Spring and winter bird populations in a Douglas-fir forest sere. J. Wildl. Manage. 51:586-595.

NORTHWEST SCIENCE

Information for Authors

Scope of Articles

The pages of *Northwest Science* are open to original and fundamental research in the basic, applied, and social sciences. *Northwest Science* does not generally publish notes or review articles. All submissions are refereed, usually by two reviewers. Papers are welcome from authors outside of the Pacific Northwest, but at least one author of any paper considered for publication must be a member of the Northwest Scientific Association.

Manuscripts

General Instructions: Submit four copies of the paper (including tables and figures) to the Editor. Manuscripts should be typewritten on 8-1/2 x 11 inch paper, double-spaced throughout (including abstract, acknowledgments, literature cited, tables, and legends for figures); ample margins must also be provided. Unnecessary footnotes should be avoided.

The manuscript should consist of sections in the following sequence:

- Title Page
- Abstract
- Text (Introduction through Acknowledgments)
- Literature Cited
- Footnotes
- Tables
- Figure Legends
- Figures

Maximum article length for papers published in *Northwest Science* is 16 journal pages. Two typed pages are approximately equal to one journal page.

Numerals will be used to indicate footnotes unless such usage would be confused with numerical data. In this situation, lowercase letters should be used. Do not break, or hyphenate, words at the ends of lines. Words to be italicized should be typed in italics.

The format and style of manuscripts should conform to general usage in recent issues.

Title Page: The first page of the manuscript should contain:

- Author's name (or names)
- Institutional address from which manuscript emanated, including city, state or province, postal code
- Title of paper
- Running head
- Total number of text figures and tables
- *Correspondence to:* List name, full address, telephone number, fax number, and e-mail address of the individual to whom correspondence should be sent.

Abstract: The purpose of an abstract is to briefly summarize the study so it is quickly accessible to the general readership of the journal. The abstract, written in complete sentences and not exceeding 250 words, should precede the text on a separate page. Authors are reminded of the diverse disciplines and readership served by the journal. With this in mind the abstract should have three parts of unequal length. First, the abstract should begin with a statement of the purpose of the study that indicates *why the study was undertaken.* Next the experimental design or approach should be stated and the *results summarized.* The abstract should end with a sentence or two on the larger significance of the research. Authors are strongly encouraged to give the abstract proper attention.

Text: Literature citations within the manuscript text should contain the author's name and year of publication, using formats A and B.

- Format A:
  ...studied by Jones (1978)...
  ...studied by Smith and Brown (1979)...
  ...studied by Smith et al. (1980)... (if more than two authors in a citation)
- Format B:
  ...was previously investigated (Smith 1965, Jones 1971, Harris 1982)...

...results of other investigations (Smith 1966, 1970; Jones 1973; Brown 1974)...

Numbers from one to nine will be spelled out, while arabic numerals will be used for numbers 10 and larger. Exceptions to this rule are: 1) a series of "mixed" numbers (e.g., 14 elk, 35 deer, 2 bobcats, and 1 bear); 2) when the number immediately precedes an abbreviation for a standard unit of measure (e.g., 3 g, 18 mm, 300 m^2). Numerals will also be used for dates, times, page numbers, and percentages.

Present all data in international (SI) unites. English equivalents may be added parenthetically. Use the 24-hour clock (0600 and 2230) and continental dating (17 November 1986).

On first mention, a species should be designated by common name followed by systematic binomial (italicized). Common names for species should not be capitalized except when derived from a proper name. Thus, "mountain hemlock" or "white-crowned sparrow," but "Douglas-fir" or "Clark's nutcracker." For abbreviations and forms of titles for serial publications, follow the BIOSIS List of Serials. Consult with the Council of Biology Editors *CBE Style Manual,* 4th ed., for general information on manuscript preparation.

Literature Cited: Only the *first letter* of the *first word* of journal articles, technical reports, theses, etc. are capitalized. First letters of *major words* in book titles are capitalized. All authors of a title are listed in the bibliographic citation ("et al." is used only in the body of the text).

Citation of unpublished reports is discouraged. Rather, cite the sources as a personal communication from the senior author (P. W. Smith pers. comm.).

Citations should be double-spaced and listed in alphabetical order at the end of the article. Listed below are some typical citations.

Journal articles

Broadbooks, H. E. 1970a. Home range and territorial behavior of the yellow pine chipmunk *Eutamius amoenus.* J. Mammal. 51:310-326.

_____. 1970b. Populations of the yellow pine chipmunk, *Eutamius amoenus.* Amer. Midl. Nat. 83:472-488.

Ceska, A., and H. Romer. 1971. A computer program for identifying species group. Vegetatio 20:48-73.

Grizze, J. E., C. F. Starmer, and G. G. Kuch. 1969. Analysis of categorical data by linear models. Biometrics 25:489-504.

Monographs or books

Jennings, H. S. 1906. Behavior of the Lower Organisms. Columbia University Press, New York.

Papers in proceedings or symposia

Ryland, J. S. 1975. Parameters of the lophophore in relation to population structure in a bryozoan community. *In* H. Barnes (ed.) Proc. 9th Eur. Mar. Biol. Symp., Aberdeen University Press, Aberdeen. Pp. 363-393.

Theses, dissertations, personal communications, and articles in press

Donald, D. B. 1971. The limnology of the plankton of three temporary pons in Alberta. University of Calgary, Calgary. M.S. Thesis.

Wiser, H. C. 1961. Decomposition and homogeneity of continua on 2-manifolds. University of Utah, Salt Lake City. Ph.D. Dissertation.

Danwiddie, P. W. In Press. Dichotomous key to conifer foliage in the Pacific Northwest. Northw. Sci.

Technical Bulletins

Daubenmire, R., and J. B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. Wash. Agric. Exp. Sta. Tech. Bull. 60. Washington State University. 210 p.

Goodwin, J. G., Jr., and C. R. Hungerford. 1979. Rodent population densities in pine forests. USDA For. Serv. Res. Pap. RM-214. Rocky Mtn. For. Range Exp. Sta., Fort Collins, Colorado. 39 p.

Footnotes: Footnotes to the text should be limited as much as possible and must be numbered consecutively. The corresponding numbers must be clearly indicated in the text.

Tables: All tables must be cited in the text, but typewritten (double-spaced) on separate pages. When submitting tables electronically, they should be presented in the simplest tabular format possible, and placed in a separate file from text.

Figures: All figures must be cited in the text. To achieve greater published fidelity, it is preferable for the printer to work directly from original photographs or drawings. Thus, original artwork or black & white glossy prints of photographs must be submitted for reproduction. When sent, be sure to include enough firm backing (e.g., lettering board) to protect them from damage. Artwork and lettering should be large enough (but not overly large) to provide clarity after a 50% reduction in size for printing. *The author's name and figure number should be penciled on the back of each illustration.* Provide a scale for distance

on map illustrations. Legends for illustrations should be typed as a group and placed on a separate page. In reference to figures and tables the words "Figure" and "Table" should be spelled out and capitalized as follows:

- ...experimental sites as indicated in Figure 2...
- ...correlation between temperature and biomass (Table 3)...

Artwork, photography, and camera ready art cannot be returned to the author.

Editing—The Editor reserves the right to edit manuscripts for grammatical correctness and clarity.

Submission of Final Copy—Manuscripts accepted for publication must be submitted in electronic copy as well as hard copy. Authors will receive instructions from the Editor regarding acceptable word processing software.

Publication Agreement—Each author or group of authors must sign a Publication Agreement provided by the Editor before their submission will be published in the journal.

Galley Proofs and Reprints—One set of proofs will be sent to the indicated author for correction shortly before publication; proofs should be returned to the Editor within *three days* of receipt. Authors should inform the Editor of any change of address for handling proofs. Reprints must be ordered when the proofs are returned. A schedule of reprint prices will be sent to the author with the proofs. Allow 8 weeks for delivery after the journal issue carrying the article appears.

Page Charges—Page charges are currently $60 per printed page. A bank draft, money order, or institutional purchase order to cover page charges and optional reprints should be submitted to the Editor upon return of galley proofs.

Correspondence—All correspondence regarding manuscripts will be between the corresponding author and Editor.

Reviewers—The associate editors reserve the right to select reviewers of their choice.

Revised November 1996

Join
The Northwest Scientific Association

A membership in the Northwest Scientific Association carries several benefits including subscription to the quarterly professional journal, *Northwest Science.*

Northwest Science is a refereed journal that has published original research in the basic, applied, and social sciences for over seventy years. Distributed throughout the Pacific Northwest, the United States, Canada, and more than fifty countries, *Northwest Science* reaches an international audience.

Members of the Northwest Scientific Association help support research and scholarship across a wide range of disciplines. Members also help underwrite scientific investigations through the Association's Research Grant Fund for graduate and undergraduate students. The annual meeting of the Association includes invited symposia as well as contributed paper sections.

Membership in the Northwest Scientific Association includes a subscription to *Northwest Science* and can be obtained by paying the appropriate dues (listed below). In addition to regular quarterly issues, members also receive occasional special issues focusing on particular scientific topics.

Inquiries concerning submissions for the journal should be directed to the Editor, whose address is listed in the inside front cover of the journal.

Clip and mail

I would like to join the Northwest Scientific Association and receive the quarterly publication *Northwest Science*.
Enclosed is a check or money order for membership dues for one year as a(n):

- ❑ Regular member ($25.00)
- ❑ Student member ($10.00)
- ❑ Institutional member ($40.00)
- ❑ Sustaining member ($40.00)
- ❑ Sustaining institutional member ($100.00)

Name

Address

City State/Province Postal Code

Dues are payable in advance and by calendar year. Please make all checks payable to the Northwest Scientific Association in U.S. currency and send to Northwest Science, c/o Washington State University Press, PO Box 645910, Pullman, WA 99164-5910, USA.

Honorary Life Members

Ewart M. Baldwin
L. C. Cady
Robert L. Carr
R. Daubenmire
R. A. Diettert
Bruce V. Ettling
William K. Ferrell
Nancy J. Grunewald
Philip Haddock
Kenneth Hammond
Adolf Hecht
Caroline Hooper
Kenneth V. Kardong
G. Brooks King
Rufus W. Kiser
Denis P. Lavender
Lewis and Clark High School Library (In memory of Thomas Large and J. G. McCracken)
Joseph W. Mills
Richard J. Naskali
Frank D. Nicol
David L. Peterson
Charles Gardner Shaw
Oscar Sziklai
Robert F. Tarrant
Ronald J.Taylor
Richard B. Walker
D. J. Wort

1998 Institutional Members

Boise State University, Boise, ID
British Columbia Institute of Technology, Burnaby, BC, Canada
Central Oregon Community College, Bend, OR
Central Washington University, Ellensburg, WA
Centralia College, Centralia, WA
College of Idaho, Caldwell, ID
Eastern Montana College, Billings, MT
Eastern Oregon State College, LaGrande, OR
Eastern Washington University, Cheney, WA
Edmonds Community College, Lynnwood, WA
The Evergreen State College, Olympia, WA
Grays Harbor College, Aberdeen, WA
Green River Community College, Auburn, WA
Idaho State University, Pocatello, ID
Lewis-Clark State College, Lewiston, ID
Lewis and Clark College, Portland, OR
Linfield College, McMinnville, OR
Montana College of MIning Science & Technology, Butte, MT
Mt. Hood Community College, Gresham, OR
North Idaho College, Coeur d'Alene, ID
Northern Montana College, Havre, MT
Oregon State University, Corvallis, OR
Pacific Lutheran University, Tacoma, WA
Pacific University, Forest Grove, OR
Peninsula College, Port Angeles, WA
Portland State University, Portland, OR
Simon Fraser University, Burnaby, BC, Canada
Skagit Valley College, Mount Vernon, WA
Spokane Falls Community College, Spokane, WA
University of Alaska, Fairbanks, AK
University of Alberta, Edmonton, AB, Canada
University of British Columbia, Vancouver, BC, Canada
University of Idaho, Moscow, ID
University of Montana, Missoula, MT
University of Oregon, Eugene, OR
University of Victoria, BC, Canada
University of Washington, Seattle, WA
Walla Walla College, College Place, WA
Washington State University, Pullman, WA
Western Washington University, Bellingham, WA
Whitman College, Walla Walla, WA

1998 Sustaining Individual Members

James K. Agee, Redmond, WA
Neil B. Armantrout, Eugene, OR
Donald J. Bedunah, Lolo, MT
Kevin R. Brown, Victoria, BC
Richard A. Cellarius, Olympia, WA
Kermit Cromack,Jr., Corvallis, OR
Diane S. Doss, Sequim, WA
George W. Douglas, Duncan, BC
Larry A. Drew, Rathdrum, ID
Rich T. Easterly, Tenino, WA
Paul A. Fishman, Portland, OR
Robert W. Gray, Sumas, WA
Robert E. Gresswell, Corvallis, OR
Frederick C. Hall, Portland, OR
Paul E. Hammond, Portland, OR
Donald P. Hanley, Seattle, WA
Randy Hein, East Wenatchee, WA
Jan A. Henderson, Mountlake Terrace, WA
Francis R. Herman, Fairbanks, AK
Barry L. Keller, Idaho Falls, ID
Karel Klinka, Richmond, BC
William N. Laval, Clarkston, WA
Giles W. Maloof, Boise, ID
Paul A. McDaniel, Moscow, ID
Howard R. Panik, Carson City, NV
Mauri S. Pelto, Dudley, MA
Steven K. Rust, Boise, ID
Penny Schaefer, Lacey, WA
Edward G. Schreiner, Port Angeles, WA
Charles G. Shaw, Auke Bay, AK
Dale Stradling, Cheney, WA
Kenneth C. Swedberg, Cheney, WA
Robert F. Tarrant, Corvallis, OR
David H. Wagner, Eugene, OR
James & Nancy Weber, Corvallis,OR
Andrea Woodward, Seattle, WA

Any member noticing information on this page that is outdated or incorrect should please bring this to the attention of the Editor.

WSU PRESS
Washington State University Press
PO Box 645910
Pullman, Washington 99164-5910 USA

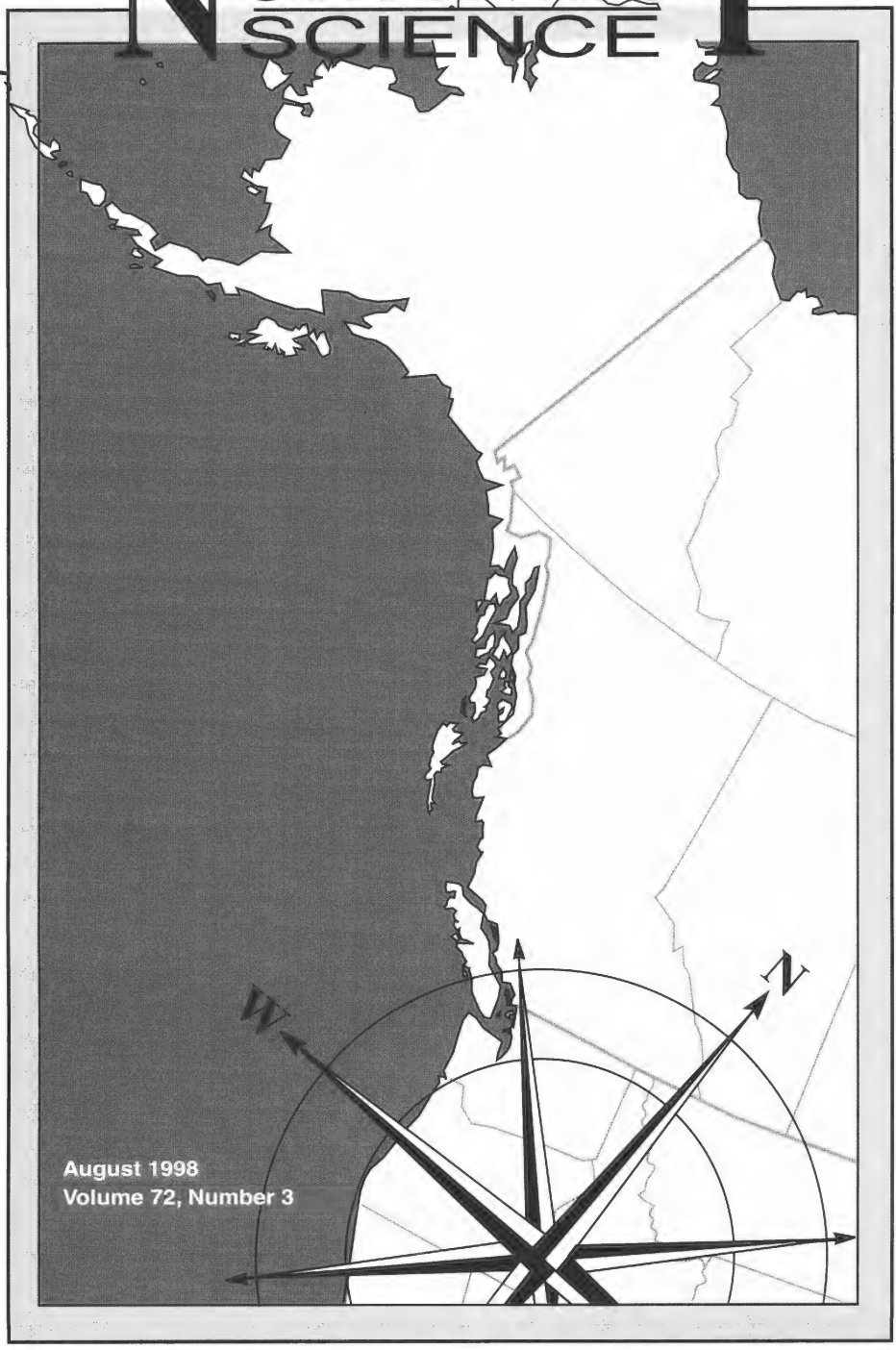
Northwest Science

Quarterly Publication of the Northwest Scientific Association

Nonprofit Organization
U.S. Postage
PAID
Pullman, WA
Permit No. 1

Papers published in **Northwest Science** are indexed in *Current Contents, Science Citation Index, Biological Abstracts, The Zoological Record, Recent Literature Supplement to The Auk, Abstracts in Anthropology, Bibliography and Index of Geology, Chemical Abstracts, Bibliography of Agriculture, Forestry Abstracts, University Microfilms, Geo Abstracts, GEOBASE,* and *Cambridge Scientific Abstracts.*

NORTHWEST SCIENCE



August 1998
Volume 72, Number 3

Northwest Scientific Association

(Founded 1923)

The Northwest Scientific Association, an affiliate of the American Association for the Advancement of Science, is an association representative of the basic and applied sciences and of social sciences.

Membership in the Northwest Scientific Association, which includes a subscription to *Northwest Science,* is open to individuals for $25 per year ($10 per year for students). Institutional membership, $40 per year. Sustaining membership, $40 per year for individuals and $100 per year for organizations, institutions, or agencies. Subscriptions are for the calendar year only.

Send membership dues, changes of address, and requests for undelivered issues to the Treasurer.

The Northwest Scientific Association is a 501-C(3) tax status organization.

Editor of *Northwest Science*

Edward G. Schreiner
USGS/BRD, Olympic Field Station
600 E Park Avenue
Port Angeles, Washington 98362
Telephone: 360-452-4501 x244
Fax: 360-452-0335
Internet: Ed_Schreiner@nps.gov

Officers of the Association

President Theodore B. Thomas
USDI Fish & Wildlife Service
Olympia, Washington (2000)*

Past President Richard Cellarius
The Evergreen State College
Olympia, Washington (1999)

Secretary Margaret O'Connell
Department of Biology MS-72
Eastern Washington University
Cheney, Washington 99004 (2000)

Treasurer David H. Hansen
Department of Biology
Pacific Lutheran University
Tacoma, Washington 98447 (2000)
Telephone: 253-535-7565
Fax: 253-536-5055
Internet: hansendh@plu.edu

Book Review Editor
Jerry O. Wolff
U.S. Environmental Protection Agency
200 SW 35th Street
Corvallis, Oregon 97333
Telephone: 541-754-4377, Fax: 541-754-4338
e-mail: wolffj@ccmail.orst.edu

Trustees:

Ross Black
Eastern Washington University
Cheney, Washington (1999)

Leonard Broberg
University of Montana
Missoula, Montana (2001)

Herbert Brown
Western Washington University
Bellingham, Washington (1999)

Sally Hacker
Washington State University
Vancouver, Washington (2001)

Charles Halpern
University of Washington
Seattle, Washington (2000)

Miles Hemstrom
USDA Forest Service
Portland, Oregon (1999)

Kenneth V. Kardong
Washington State University
Pullman, Washington (2001)

Barry L. Keller
Idaho State University
Pocatello, Idaho (1999)

John Koprowski
Willamette University
Salem, Oregon (2000)

Paul A. McDaniel
University of Idaho
Moscow, Idaho (2000)

Kurt Othberg
Idaho Geological Survey
Moscow, Idaho (2000)

Tim Reynolds
Environmental Science and Research Foundation
Idaho Falls, Idaho (2000)

Roger Rosentreter
Bureau of Land Management
Boise, Idaho (1999)

Steve Sillett
Humboldt State University
Arcata, California (2001)

Darlene Zabowski
University of Washington
Seattle, Washinton (2001)

*Term of office expires in the year given in parentheses.

© 1998 by the Northwest Scientific Association. All rights reserved.

August 1998 Volume 72, Number 3

NORTHWEST SCIENCE

Editor	Edward G. Schreiner	USGS/BRD—Olympic Field Station, Port Angeles
Managing Editor	Nancy J. Grunewald	Washington State University
Indexer	Caroline Hooper	
Associate Editors		
Anthropology	R. Lee Lyman	University of Missouri—Columbia
Aquatic Biology	Gary L. Larson	U.S. Geological Survey—Corvallis
Botany	Eldon H. Franz	Washington State University
Mathematics & Computer Applications	Steven J. Ghan	Battelle Pacific Northwest Labs—Richland
Forestry	Michael C. Feller	University of British Columbia
Geology & Geography	David R. Gaylord	Washington State University
Soils	Robert L. Edmonds	University of Washington
Wildlife Biology	Patricia J. Heglund	University of Idaho
Zoology	Richard B. Forbes	Portland State University
Book Reviews	Randall C. Morris	Envir. Sci. & Res Fdn.—Idaho Falls

ISSN #0029-344X

CONTENTS

Announcements

157 Seedfall, Seed Germination, and Initial Survival and Growth of Seedlings of *Thuja plicata* in Southwestern British Columbia—**Michael C. Feller and Karel Klinka**

170 Long-Term Trend In Marbled Murrelets In Southeast Alaska Based On Christmas Bird Counts—**Gregory D. Hayward and George C. Iverson**

180 Factors Affecting the Success of California Poppy (*Eschscholzia californica*) Introduced into Western Washington State—**H. Elizabeth Kirkpatrick**

190 Browsing Ungulates—An Important Consideration in Dieback and Mortality of Pacific Yew (*Taxus brevifolia*) in a Northeastern Oregon Stand—**Catherine G. Parks, Larry Bednar, and Arthur R. Tiedemann**

198 Exotic Plant Records in the Northwest United States 1950-1996: an Ecological Assessment—**J. Christopher Toney, Peter M. Rice, and Frank Forcella**

214 Occurrence of Windthrow in Forest Buffer Strips and its Effect on Small Streams in Northwest Washington—**Jeffrey D. Grizzel and Noel Wolff**

Northwest Science Forum

224 Challenges and Opportunities in Collaborative Natural Resource Management—**Clare M. Ryan**

Book Reviews

228 *Land Mammals of Oregon* by B. J. Verts and Leslie N. Carraway—**reviewed by Jerry Wolff**

230 *American Pronghorn: Social Adaptations and the Ghosts of Predators Past* by John A. Byers—**reviewed by Scott Creel**

232 *The Great Blue Heron* by Robert W. Butler—**reviewed by Matthias Leu**

234 *Preserving Nature in National Parks: A History* by Richard W. Sellars—**reviewed by David L. Peterson**

236 *White Goats White Lies: The Abuse of Science in Olympic National Park* by R. Lee Lyman—**reviewed by R. Gerald Wright**

239 *Wild To The Last* by Charles Pezeshki—**reviewed by Marv Hoyt**

Northwest Science Information for Authors

Announcements

1999 Annual Meeting

Washington State Historical Society and University of Washington, Tacoma Campus
Tacoma, Washington, March 24–27, 1999

The 72nd annual meeting of the Northwest Scientific Association will be hosted by the Washington State Historical Society and the University of Washington, Tacoma Campus, Tacoma, Washington. The meeting will be held jointly with the National Park Service to commemorate a Century of Stewardship at Mount Rainier National Park, and the Lichen Guild, on March 24-27, 1999. Following a business meeting of the Governing board on March 24, scientific sessions, including plenary sessions will occur on the following two days with a variety of concurrent sessions and symposia. Preliminary plans are to hold symposia on: geologic history of Cascade volcanoes, forest-habitat relations, and invasion and management of non-native species. An opening plenary session on Mount Rainier National Park and its role in scientific investigations is scheduled for the meeting. Field trips to local and regional ecological sites forming a continuum from Mount Rainier to Puget Sound will be offered, including field trips to low-elevation, old-growth forests at Mount Rainier National Park, managed forests at Pack Forest, and the Nisqually Wildlife Refuge, at the mouth of the Nisqually River.

Members from all sponsoring organizations as well as non-members are welcome to participate in the meeting. Students are especially encouraged to attend and report the results of their research at the meeting. The call for abstracts and registration information will be mailed to all members of the Association by early October, 1998.

Information about the meeting may be obtained from Kristen Scheyer, Program Coordinator, Continuing Education, College of Forest Resources, University of Washington, Seattle, Washington 98195; the e-mail address is kscheyer@u.washington.edu.

1999 Student Research Grants

The Northwest Scientific Association annually awards research grants in support of student research. Applicants must be student members of the Northwest Scientific Association at the time they submit their proposal (see inside front cover for information about joining the association).

Proposals should be prepared with the following format:

A cover page that includes:

- Title
- Name, address, phone number, and e-mail of the applicant and associated institution
- Name of major professor/advisor
- Amount of money requested (maximum $1000)

The body of the proposal should include:

- Title
- Statement of justification (purpose, objective(s), and hypotheses)
- Methodology/experimental design (including methods of analysis)
- Detailed budget on a separate page (no salaries)

The text of the proposal should be no more than three (3) double-spaced pages (12-pt. font, not including the title, literature cited, and budget pages).

Continued, next page

Four copies of the proposal are due to Dr. Ross Black on or before January 15, 1998.

Dr. Ross Black
Department of Biology, MS 72
Eastern Washington University
Cheney, Washington 99004
Phone (509) 359-4815
Email:rblack@ewu.edu

Grant winners will be announced at the annual meeting of the Northwest Scientific Association held at Washington State Historical Museum and the University of Washington, Tacoma Campus, Tacoma, Washington, March 24-27, 1999.

Awards provided by the Northwest Scientific Association are designed to help students complete research projects in the basic and applied sciences. Awards should be used only to support research activities of the student. Grant support can not be used for salaries. Students will be expected to present the results of their research at a future NWSA meeting.

Book Review Editor Changes

This is the last issue in which Jerry O. Wolff will appear in the editorial masthead of *Northwest Science*. Jerry has accepted a position as Professor and Chairman of the Department of Biology at the University of Memphis where he is beginning a new research program and "adjusting" to new obligations as an administrator. Jerry assures us that his first semester is going quite well and that he will periodically return to the Northwest to continue work on small mammal behavioral and ecotoxicological studies with Dan Edge at their field site near Corvallis, Oregon.

Jerry O. Wolff has been an active and valued member of the Northwest Scientific Association for the last five years. In addition to serving as Book Review Editor, he also was a member of the Board of Trustees and served on the Student Awards committee for four years (chair for three years).

Jerry, please accept our sincere thanks for your years of dedicated service to the Northwest Scientific Association and to our journal. We all wish you well in your new endeavors. Please stay in touch

Please join me in welcoming our new Book Review Editor, Dr. Randall C. Morris. Randy is already hard at work obtaining reviews for the November issue of *Northwest Science* and intends to live up to the high standards set by Jerry Wolff. Randy would very much like feedback from readers as to what kinds of books they would like to see reviewed. You can communicate directly with Dr. Morris at the Environmental Science and Research Foundation, Inc., 101 S. Park Ave., Suite 2; P. O. Box 51838, Idaho Falls, Idaho 83405-1838. e-mail morrisr@esrf.org. Thanks are due to our Editorial Committee for finding a new Book Review Editor so quickly.

Michael C. Feller and **Karel Klinka,** Faculty of Forestry, Department of Forest Sciences, University of British Columbia, Vancouver, B.C. Canada V6T 1Z4

Seedfall, Seed Germination, and Initial Survival and Growth of Seedlings of *Thuja plicata* in Southwestern British Columbia

Abstract

Reasons for the relative absence of *Thuja plicata* regeneration in the old growth *Thuja plicata - Tsuga heterophylla* forests close to Vancouver, British Columbia, were assessed by measuring seedfall and applying *Thuja* seeds to small plots. All measurements were replicated in two different sites. The small (0.5 m^2) plots were established in 2 canopy cover conditions (clearcut and forest), 3 seedbed conditions (mineral soil, burned forest floor, and undisturbed forest floor), and 2 mammal and bird seed predation conditions (with and without). Each canopy cover, seedbed, and seed predation combination was replicated 15 times in each study site. Large numbers of viable seeds (>200/m^2) fell in 1990/91 and again in 1994/95. Seed germination decreased in the order – burn > mineral soil > forest floor; forest > clearcut; and without predation > with predation. After 3 growing seasons, of the 100 seeds applied to each plot, an average of only 1-2 seedlings had survived. This number of surviving seedlings decreased in the order – burn > mineral soil > forest floor, and clearcut > forest, but was not influenced by predation. After 3 growing seasons, seedling growth tended to decrease in the order – burn > forest floor > mineral soil; clearcut > forest; and without predation > with predation.

It was concluded that the relative lack of regenerating *Thuja* seedlings in the study area forests was not due to a lack of viable seeds. Although a lack of suitable seedbeds and the presence of the forest canopy reduce the number of seedlings in undisturbed forests, this number should still be substantial. The observed relative lack of regenerating *Thuja* seedlings must therefore result from other factors which were not considered in the present study.

Introduction

Thuja plicata (western redcedar, hereafter abbreviated as *Thuja*) is a prominent tree species in the Coastal Western Hemlock zone forests of British Columbia (Krajina 1969). It is considered to have a high shade tolerance (Minore 1990). Although earlier work (Krajina et al. 1982, Minore 1990) suggested that it was less shade tolerant than its common associate, *Tsuga heterophylla* (western hemlock), more recent work in British Columbia suggests the opposite (Carter and Klinka 1992, Wang et al. 1994). Because of this shade tolerance and its longevity, it is considered to be a climax species (Minore 1990).

A climax species is expected to have an abundance of regenerating young seedlings within an old growth forest. Observations of *Thuja*-dominated old growth forests near Vancouver, B.C. suggested a relative lack of young *Thuja* seedlings. This led to a multifaceted study of the ecology of *Thuja* in these forests. One facet involved quantifying the structure of the forests. This was completed by Daniels et al. (1995) who confirmed that the forests contained extremely few *Thuja* trees less than 100 years old. A surprising lack of *Thuja* regeneration has also been observed elsewhere in B.C., Alaska, and Idaho (Minore 1983, Parker and Johnson 1994). Based on measured irregular age class structures and occurrence of distinct peaks in age classes of *Thuja*, Daniels et al. (1995) concluded that conditions for *Thuja* regeneration had varied with time and hypothesized that regeneration peaks occurred following fire or windthrow events. Eis (1962) had also previously hypothesized that regeneration in these forests peaked following fire.

Some studies reported that disturbed seedbeds were preferred by *Thuja* for regeneration from seed (Minore 1990) and were consistent with the preceding hypothesis. The results of other studies, however, were inconsistent with the hypothesis. These studies, in U.S. inland northwest forests, found that decaying wood in contact with mineral soil could be the preferred seedbed in old *Thuja* forests (Parker, 1986), and that *Thuja* regeneration was more abundant in untreated areas than in mechanically treated or burned ones (Ferguson 1994). In forests close to Vancouver, Soos and Walters (1963) found that seedbed type had little influence on the quantity and rate of *Thuja* germination, but in clearcut areas germinant

© 1998 by the Northwest Scientific Association. All rights reserved.

survival was better on mineral soil and burned substrata than on decaying wood.

Recognizing that a study of stand structure alone, in conjunction with some of the *Thuja* germination contradictions in the literature, could not conclusively explain the dynamics of *Thuja* in the Vancouver region, we embarked on additional ecological studies of *Thuja*. Wang et al. (1994) have reported the influence of light on *Thuja* seedling growth. The present report focuses on the earliest stage of *Thuja* regeneration – seedfall, seed germination, and initial growth and survival of *Thuja* seedlings.

The objectives of the study were to determine for the Vancouver region forests 1) if the relative lack of regenerating *Thuja* seedlings was due to a lack of viable seeds, and 2) the influence of light, forest floor disturbance, and predation by birds and mammals on *Thuja* seed, germination, and initial growth and survival of *Thuja* seedlings.

Methods

Study Area and Field Work

Two study sites were established, one in Capilano watershed (Eastcap Creek) and another in Coquitlam watershed (Cedar Creek), two of Vancouver's water-supply watersheds managed by the Greater Vancouver Watershed District. The study sites are located 20 km north (Eastcap Creek), and 30 km northeast (Cedar Creek) of the city of Vancouver, British Columbia. Both sites were located within the Very Wet Maritime Coastal Western Hemlock biogeoclimatic subzone which is characterized by a perhumid, cool, mesothermal climate (Klinka et al. 1991). Both sites were on lower, concave slopes, averaging 10 - 15% slope, and contained coarse-skeletal Humo-Ferric Podzols (Canada Soil Survey Committee 1987) analogous to U.S. Typic Haplorthods (Soil Survey Staff 1975) derived from glacial till and underlain by granitic rocks. The Eastcap Creek site had an elevation of 500 m a.s.l. and a northerly aspect, while the Cedar Creek site had an elevation of 600 m a.s.l. and a southeasterly aspect.

Each study site contained a recent ($\leq$ 3 years old) clearcut and an adjacent old growth forest with little *Thuja* regeneration but abundant overstory *Thuja*. The Eastcap Creek forest had a total basal area of 82 m^2/ha comprised of 30 m^2/ha of *Thuja*, 50 m^2/ha of *Tsuga heterophylla*, and 2 m^2/ha of *Abies amabilis* (amabilis fir). The Cedar Creek forest had a total basal area of 173 m^2/ha comprised of 159 m^2/ha of *Thuja*, and 14 m^2/ha of *Tsuga heterophylla*. The dominant and codominant layers of the tree canopy contained 18 stems/ha of *Thuja*, 265 stems/ha of *Tsuga*, and 42 stems/ha of *Abies* in the Eastcap Creek forest, and 83 stems/ha of *Thuja* and 158 stems/ha of *Tsuga* in the Cedar Creek forest. Tree regeneration in these forests (seedlings up to 100 cm high) comprised 36 stems/ha of *Thuja*, 10,670 stems/ha of *Tsuga*, and 5,670 stems/ha of *Abies* in the Eastcap Creek forest, and 224 stems/ha of *Thuja* 7,390 stems/ha of *Tsuga* and 2,170 stems/ha of *Abies* in the Cedar Creek forest. Understory vegetation in the forests consisted of very sparse shrub and herb layers over a moss layer varying in cover from 0 to 90%. Shrub, herb and moss vegetation in the clearcuts was initially similar to that in the forest although herb and shrub cover increased during the study.

Seedfall was collected in perforated plastic greenhouse trays (27 cm x 53 cm x 6 cm deep) lined with fiberglass insect screen. At each site the trays were placed at 20 m intervals along two transects 20 m apart, oriented at right angles to the forest-clearcut edge. Placement began 20 m either side of the edge, with 5 trays per transect in the clearcut and 5 in the forest. Thus, at each site a total of 10 trays was placed in the forest, and 10 in the clearcut. Trays were in place from August 1990 until June 1995. They were emptied every 2-4 weeks during the September-May period, or whenever possible during periods of snow, and every 6 weeks during the June-August period.

Seed germination was studied using small square plots, 0.5 m^2 in area. At each study site, plots were located randomly between obstacles (primarily decaying wood) both in the forest and in the clearcut, all plots being at least 30 m from the forest-clearcut edge. One third of the plots in each canopy cover situation were located on undisturbed forest floors, another third had all forest floor material removed to expose the surface mineral soil, and the last third were located on burned forest floors. The burned forest floor was achieved by piling woody debris < 7 cm diameter on the forest floor surface during dry periods in July - August, 1990, covering the debris with

plastic sheets, then burning with a hand-held drip torch in November, 1990, when the surrounding organic materials were very wet. Forest floor depths of burn (amount of forest floor burned by the fires) were monitored using 3 or 4 depth-of-burn pins in every second plot. Depths of burn ranged from 0 to 21 cm, but averaged 1.9 cm at Eastcap Creek and 1.0 cm at Cedar Creek based on 96 measurements per site. Undisturbed forest floor depths averaged 10-25 cm. Half of the plots of each seedbed type in each light situation were fitted with metal wire (1 cm mesh) cages to exclude mammal and bird, but not insect seed predators. Each canopy cover/seedbed/predation combination was replicated 15 times. Thus, there was a total of – 2 (study site) x 2 (canopy cover) x 3 (seedbed) x 2 (predation) x 15 (replicates) = 360 plots.

Seedbed and predation treatments were randomly allocated to the plots. All plots were prepared during July – August, 1990, and covered with fiberglass screen to exclude fresh seedfall immediately after preparation. Fiberglass screen was placed on the burned plots within a few hours of burning. Within a week of burning 100 *Thuja* seeds collected from nearby areas (B. C. Ministry of Forests Seed Center, seedlot number 10326) were scattered onto the ground surface in each experimental plot. Germination tests indicated these seeds had a viability of 89%.

The percentage of above-canopy photosynthetically active radiation reaching the ground surface in the forests was measured on a uniformly cloudy day in July and again in August, 1997, using a Decagon Devices, Model SF-40 sunfleck Ceptometer. Measurements were made every 5 m on a 50 x 50 m square grid containing the seed germination plots. Due to the lack of tree mortality in the plots during the 1991 – 1997 period and the relatively slow growth rates of vegetation in old growth forests, the August 1997 measurements are considered to represent light conditions during the study.

During the 1990/91 winter, tree blowdown in the Eastcap Creek forest resulted in the loss of 3 plots. Water erosion at Cedar Creek resulted in the loss of 2 plots in the forest and 13 in the clearcut. These plots were excluded from subsequent analysis. By mid-May, 1991, *Thuja* seedfall had declined to very low levels, so the fiberglass screens were removed from the plots. This occurred within 2 weeks of snow leaving the plots. The numbers of living and dead *Thuja* seedlings in each plot were counted once every 2-3 weeks until mid-September, 1991, with the final count for the year occurring on 17 October. At this time all living seedlings were marked with colored toothpicks to avoid confusion with seedlings from fresh seedfall in subsequent years. The metal seed predator exclosures were removed in August when predation was considered to have dropped to very low levels (T. Sullivan, Faculty of Forestry, University of B. C.: pers. comm.).

Seedlings were counted on 7 February, 1992, then again in late March and every 3-4 weeks until the end of October. In 1993, seedlings were counted on 22 April, then every 6-8 weeks until the end of September. Plots were weeded regularly, as needed, to eliminate plant competition as a variable influencing the results.

In October, 1993, all surviving seedlings had their basal diameters, heights, and crown volumes (greatest width (A) x width at 90° to A x height) measured.

Laboratory Work and Data Analysis

Seeds collected in the seedfall traps were dried at 25 - 30° C in the laboratory, separated from other litterfall, counted, then tested for viability on a germination table.

Data on the total number of seeds germinating and the number of living seedlings at each counting period were subjected to analysis of variance (ANOVA). In some instances, visual inspection suggested that datasets were not normally distributed and/or Bartlett's tests indicated variances were not homogeneous. These datasets were subjected to different transformations and the transformed data again subjected to ANOVA. Transformations improved normality and homogeneity of variances although occasionally variances were still not homogeneous. Seedling growth data were also subjected to checking for normality and homogeneity of variances prior to ANOVA. Logarithmic transformations were needed to improve normality and homogeneity of variances but some datasets could not be transformed in such a way as to meet the assumptions of ANOVA. The two study sites were not replicates as they had different aspects with noticeably different microclimates. Consequently, analyses of variance were 3 way factorials, with seedbed, light,

and predation as the 3 factors. All analyses were conducted separately for each study site using SYSTAT software (Wilkinson 1986).

Results and Discussion

Seedfall

During the study, high seedfall years occurred in 1990/91 and 1994/95 (Figure 1). The number of viable seeds reaching the ground surface in the forests was >200 seeds/m^2 at Eastcap Creek and >1000 seeds/m^2 at Cedar Creek during the study. This shows that the low density of *Thuja* seedlings in the forests can not be attributed to a lack of viable seeds. Most *Thuja* seeds are reported to escape bird and animal predation (Minore 1990) and viable seeds, if they do not germinate, may enter the forest soil seed bank. Studies of seed banks in western North American forests containing *Thuja* have found viable *Thuja* seeds present (Harmon and Franklin 1995, McGee and Feller 1993, Yearsley 1993). Even if germination is unlikely after a year in the seedbank (Minore 1990), the widespread presence of viable *Thuja* seeds in soil seedbanks further suggests that the low number of *Thuja* seedlings in *Thuja* forests can not be attributed to a lack of viable *Thuja* seeds.

Seed Germination

The total numbers of seeds germinating (Table 1) were only slightly greater than the maximum numbers of living germinants recorded (Figures 2-4). The trends in numbers for seedbed, light, and predation, were identical for both study sites. The only significant first or second order interaction for both study sites was between seedbed and predation. However, in neither case did this interaction alter the observation that, for both study sites, the numbers of seeds germinating decreased in the order - burn>mineral soil>forest floor in both the presence and absence of predation. The interaction only influenced the relative magnitude of the differences.

Thus, germination decreased in the order - burn>mineral soil>forest floor; forest>clearcut; and without predation>with predation. Germination was also greater at Cedar Creek than at Eastcap Creek. At Cedar Creek, the average total number of seeds germinating per plot for burned plots in the forest without predation was 80, and close to the potential maximum of 89. Greater germination at Cedar Creek is consistent with the greater quantities of *Thuja* present in the Cedar Creek forest. In the field, germination was greater in the forest than in the clearcut. The forested plots

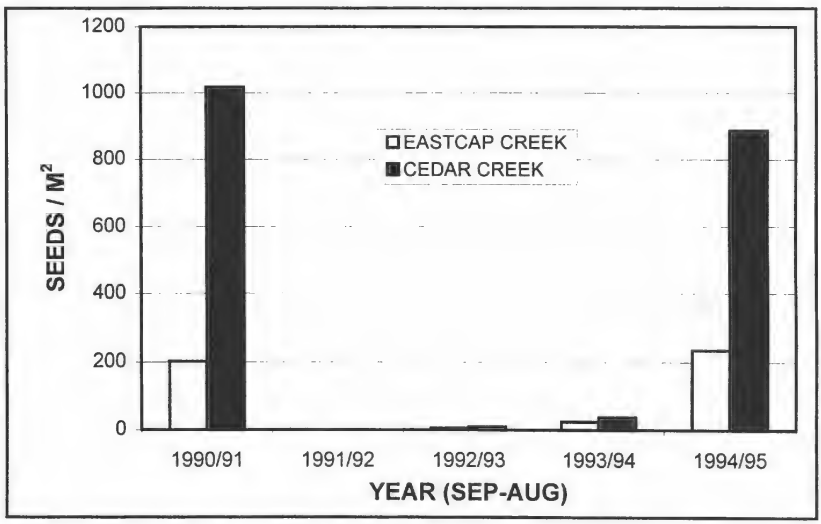


Figure 1. Annual (1 September - 31 August) number of viable seeds falling in the forests in each of the two study areas.

TABLE 1. Mean total number of germinating seeds per plot, and results of analyses of variance.

Environmental parameter	Eastcap Creek	Cedar Creek Creek
1. Seedbed (S)		
Mineral soil	13 (1)[b]	34(3)[b]
Burned forest floor	25(2)[a]	59(4)[a]
Undisturbed forest floor	8(1)[c]	15(3)[c]
Significant interactions	S x P	S x P
2. Canopy Cover (C)		
Forest	18(2)[a]	43(3)[a]
Clearcut	14(2)[b]	27(3)[b]
Significant interactions	none	none
3. Predation (P)		
Without	18(2)[a]	46(3)[a]
With	14(1)[b]	24(3)[b]
Significant interactions	S x P	S x P

For a given area and environmental parameter, different superscripts indicate significantly different ($P<0.05$) numbers of seedlings per plot. Standard errors are given in parentheses.

received 1 - 12% (average 4% at Cedar Creek and 2% at Eastcap Creek) of the photosynthetically active radiation received by the clearcut plots. The fact that laboratory germination can be improved by exposing seeds to light (Li et al. 1994) suggests that the influence of the forest canopy on light is outweighed by its influence on other environmental factors, with respect to *Thuja* seed germination.

Seedling Survival

Numbers of living seedlings peaked early in the first growing season with 74-93% of total mortality occurring during the first growing season (Figure 5). Mortality during the first winter dropped to 4-22% of the total, while mortality during the next 2 years accounted for only 1-11% of the total at Eastcap Creek and 1-4% of the total at Cedar Creek (Figure 5). Seedling survival after 3 growing seasons varied from almost 0 (forest floor seedbeds at Cedar Creek) to 11% (clearcuts at both study sites) of the number of seeds that germinated. On average, only 1 and 2 seedlings of the potential 89 per plot, at Eastcap and Cedar Creeks., respectively, survived the first 3 years.

The two time periods with the greatest mortality in the present study were 25 June - 10 July and 20 August - 17 October, 1991, (Figures 2-4) and they coincided with low rainfall periods. Only 4 mm of rain during a 14 day period in the June-July sampling interval, and 2 mm of rain during a 32 day period in the August-October sampling interval were recorded at a weather station located at a similar elevation 9 km southeast of the Cedar Creek site. This weather station recorded 33 – 97 mm of rain during each of the other sampling intervals and no less than 37 mm of rain during any other 14 day period in the 1991 growing season. Surface soil temperatures were not measured but no stem lesions were seen above the ground line (cf. Gashwiler 1971), suggesting water deficits, rather than heat, as the major cause of mortality. Minor, but unquantified amounts of frost heaving and frost damage were observed, contributing to the winter period mortality. Most mortality, however, was probably attributable to water deficits during the first growing season, which is consistent with previous studies of *Thuja* seedling survival (Gashwiler 1971, Soos and Walters 1963) and with the known preference of *Thuja* for moister sites (Krajina 1969).

Low survival of seedlings during the first growing season has been reported previously for *Thuja* (Gashwiler 1971, Minore 1990, Soos and Walters 1963). Drought and high soil temperatures have been the primary causes of this mortality. High temperatures and drought are unlikely in forests. There, low survival is more likely a result of shade-induced poor root growth resulting in inadequate supply of water and nutrients to seedlings (Minore 1990).

Survival was poorest in forest floor seedbeds, being almost 0% at Cedar Creek (Figure 2). Numbers of living seedlings always decreased in the order - burned forest floor>mineral soil>forest floor, for both study sites. Mortality during the first year was sufficiently high that during the second and third years, there were generally no significant differences in the numbers of living germinants between any of the seedbed types at Cedar Creek or between the mineral soil and forest floor seedbeds at Eastcap Creek. Not only did more seeds germinate on the burned seedbeds at Eastcap Creek (Table 1) but survival was also greatest on these seedbeds (Figure 2). At Cedar Creek, greater germination on the burned seedbeds was offset by greater mortality on these seedbeds than on mineral soil seedbeds (Figure 3) accounting for the lack of a statistically significant difference in the numbers of surviving germinants between these seedbed types. These

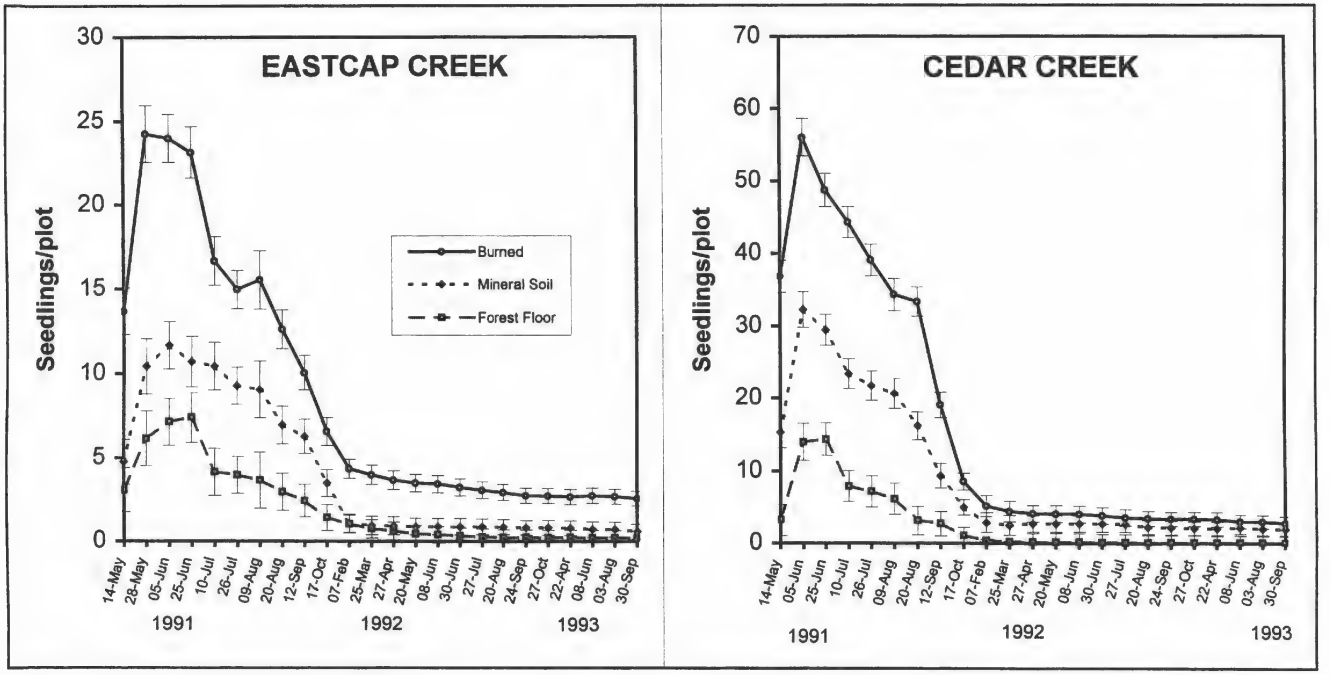


Figure 2. Mean number of living seedlings per plot as a function of time at each study site for each of the three seedbeds.

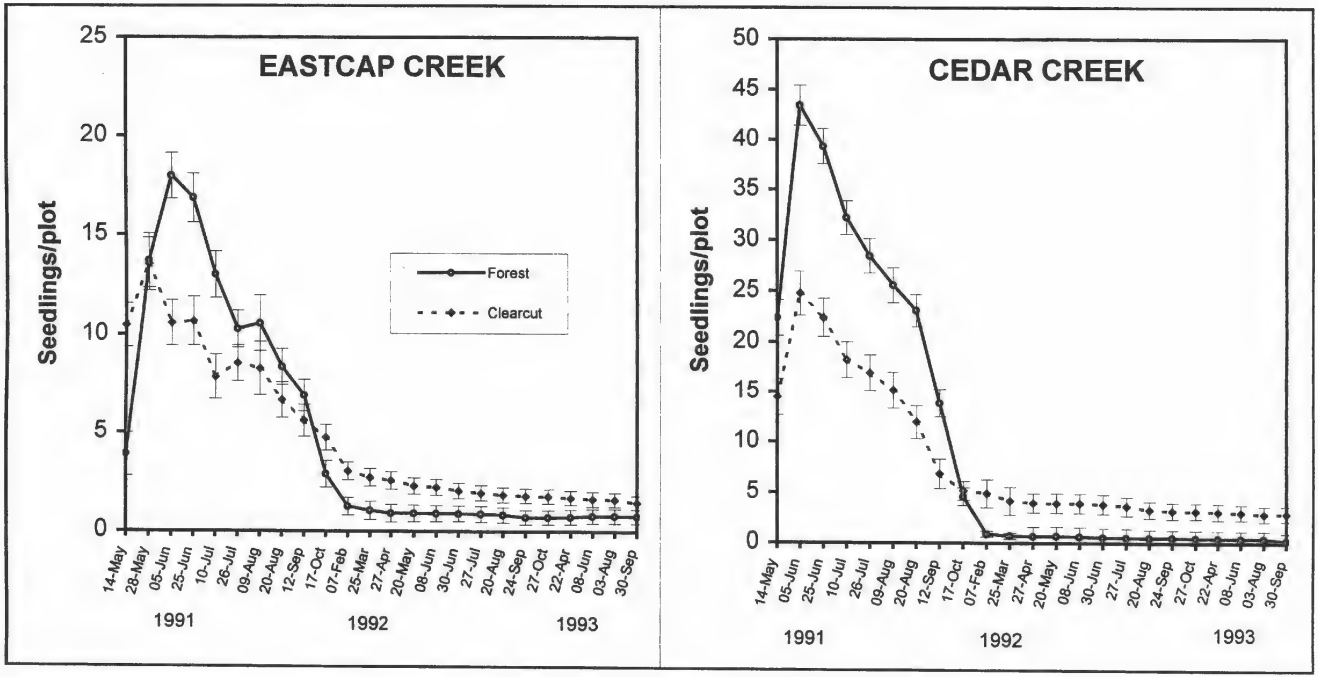


Figure 3. Mean number of living seedlings per plot as a function of time at each study site for the forest and clearcut areas.

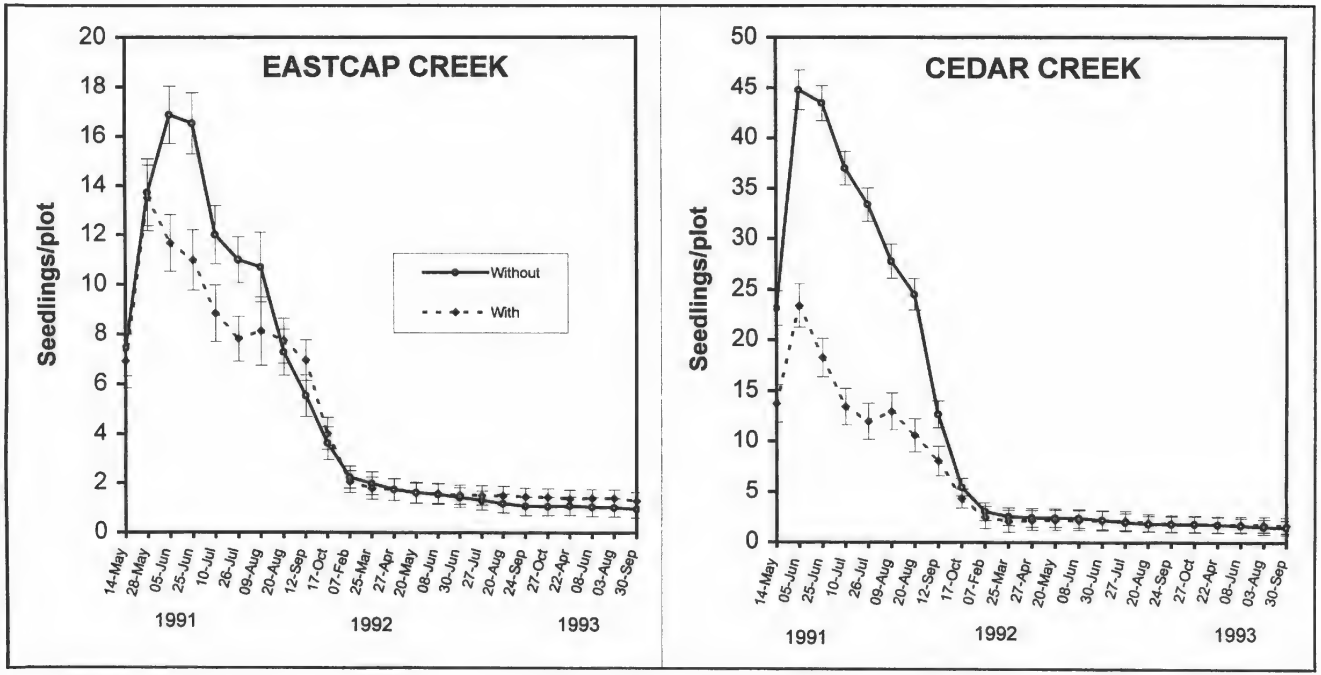


Figure 4. Mean number of living seedlings per plot as a function of time at each study site for the plots with and without vertebrate seed predators.

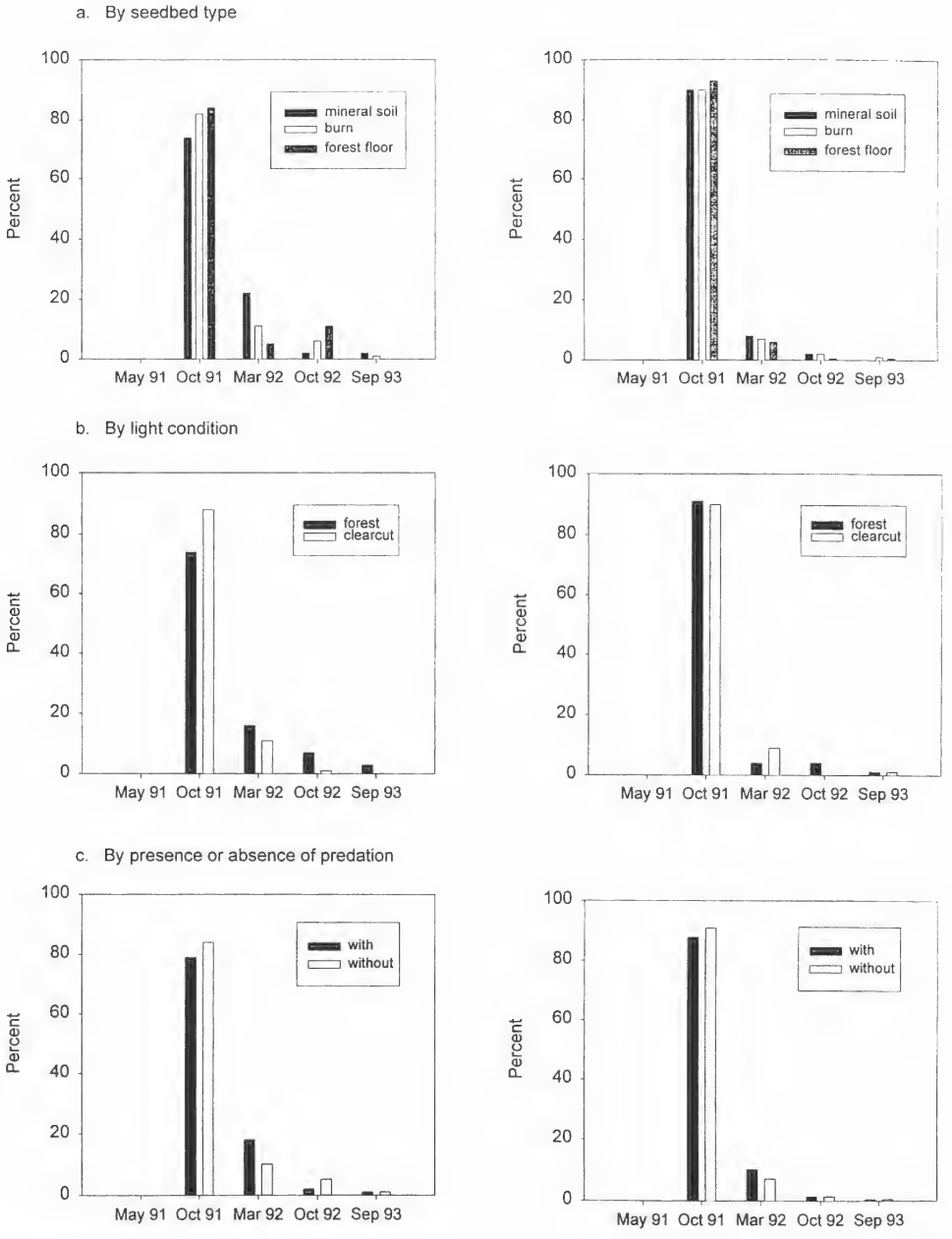


Figure 5. Mortality of seedlings expressed as a percentage of the total mortality during different time intervals during the first three years. Results for Eastcap Creek are on the left, and for Cedar Creek on the right. The time intervals are—

May 91 = 14 May – 5 June, 1991
Oct 91 = 6 June – 17 October, 1991
Mar 92 = 18 October, 1991 – 25 March, 1992
Oct 92 = 26 March – 27 October, 1992
Sep 93 = 28 October, 1992 – 30 September, 1993

results were not affected by any first or second-order interactions.

Although germination was greater in forest than in clearcut plots at both study sites during the first growing season (Table 1), the reverse trend for survival occurred at both study sites during subsequent years (Figure 3). This resulted in greater numbers of living seedlings in the forest plots during the first growing season, but greater numbers in clearcut plots during the second and third growing seasons (Figure 3). The significant differences in the numbers of living seedlings between the two canopy covers were generally more pronounced at Cedar Creek than at Eastcap Creek. By the end of the third growing season, differences were statistically significant only at Cedar Creek, with, again, no first or second order interactions.

Minore (1990) concluded that disturbed mineral soil seedbeds were a major requirement for regeneration from *Thuja* seed. He considered that burning favored *Thuja* seed germination by creating more mineral soil seedbed sites. In the present study, none of the burned plots had exposed mineral soil. No burned plot had a forest floor that was less that 3 cm thick during the first growing season. Burned forest floors in the study area were clearly the most desirable seedbed for *Thuja*. Greater numbers of *Thuja* seedlings on burned forest floor seedbeds and in clearcut rather than forest plots, suggest that *Thuja* has evolved to regenerate following disturbances which produce either mineral soil or burned forest floor seedbeds and/or expose them to greater amounts of light. In drier and hotter summer environments in the U.S. Pacific Northwest, seedling mortality from high surface temperatures in clearcuts suggests partial shading may enhance seedling survival (Gashwiler 1971, Haig et al. 1941). The influence of partial shading was not assessed in the present study, however.

The 100 seeds per plot produced 0.18 and 0.04 surviving seedlings after 3 growing seasons in undisturbed forest floor in the Eastcap and Cedar Creek forests, respectively. When applied to the number of viable seeds falling in the forest (Figure 1) this would suggest approximately 4,000 – 14,000 surviving *Thuja* seedlings per ha, 3 years after a good seed year. Even allowing for loss of seed as a result of seedfall onto rock or log surfaces, which cover approximately 30% of the ground surface in the forests of the study area (Song 1997), a substantial number of seedlings should still survive. Observations of considerably fewer *Thuja* seedlings suggest other factors, such as pre-logging wildlife browsing or understory plant competition, have influenced *Thuja* regeneration in the undisturbed old growth forests of the study area.

Predation significantly decreased the numbers of seeds germinating (Table 1), but greater mortality occurred in the plots without predation (Figure 4). This resulted in no significant influence of predation on numbers of surviving seedlings from August (Eastcap Creek) or October (Cedar Creek) of the first growing season to the end of the study (Figure 4). It is unclear why greater mortality occurred in the predator exclusion plots. These results suggest that bird and mammal seed predation may be occurring but this has little effect on the numbers of living *Thuja* seedlings beyond the first growing season.

Seedling Growth

Mineral soil was generally the poorest seedbed for growth at both study sites, although not all growth differences between seedbed types were statistically significant (Table 2). At Eastcap Creek, the best seedling growth was found on undisturbed forest floors while at Cedar Creek, seedling growth tended to be the best on burned forest floors, although for the latter area there were no significant growth differences between burned and undisturbed forest floors. The seedbed x predation interactions for height and basal diameters did not change interpretations of the results. Growth was least on mineral soil seedbeds for both predation situations, but it was statistically significantly less only when predators were present.

Some of the differences in these results between Eastcap and Cedar Creek may be an artifact of the small sample size for seedlings in undisturbed forest floors. These small sample sizes were the result of the low seed germination and seedling survival rates in the forest floors. It can be stated with more confidence that seedling growth was better in burned than in mineral soil seedbeds, with the differences being more pronounced at Cedar Creek.

Seedlings generally grew better at Cedar Creek than at Eastcap Creek, even on undisturbed forest floor seedbeds (Table 2). This better growth

TABLE 2. Mean heights, basal diameters, and canopy volumes of *Thuja* seedlings at the end of the third growing season, and results of analyses of variance.

	Eastcap Creek				Cedar Creek			
Environmental parameter	Height (cm)	Basal diameter (mm)	Canopy volume (cm^3)	n	Height (cm)	Basal diameter (mm)	Canopy volume (cm^3)	n
1. Seedbed (S)								
Mineral soil	9.1 (1.3)[b]	1.1 (0.1)	838 (245)[b]	42	9.7(1.3)[b]	1.5 (0.2)[b]	1507 (546)	40
Burned forest floor	9.2 (0.6)[b]	1.4 (0.1)	918 (170)[b]	136	18.8 (0.9)[a]	2.5 (0.1)[a]	4491 (678)	164
Undisturbed forest floor	14.6 (2.3)[a]	1.7 (0.1)	3114 (1671)[a]	14	17.3 (0.9)[a]	3.1 (0.5)[a]	2488 (1150)	6
Significant interactions	none	none	none		S x P	S x P	none	
2. Light (L)								
Forest	3.7 (0.1)[b]	0.6 (0.0)[b]	18 (3)[b]	55	3.0 (0.2)[b]	0.3 (0.0)[b]	11 (3)[b]	39
Clearcut	12.0 (0.6)[a]	1.6 (0.1)[a]	1479 (246)[a]	137	20.2 (0.8)[a]	2.8 (0.1)[a]	4744	171
Significant interactions	none	none	none		none	none	none	
3. Predation (P)								
Without	10.4 (0.9)	1.5 (0.1)[a]	1533 (399)[a]	79	17.8 (0.9)	2.5 (0.1)[a]	4472 (800)	135
With	9.1 (0.6)	1.2 (0.1)[b]	730 (124)[b]	113	15.7 (1.4)	2.0 (0.2)[b]	2773 (500)	75
Significant interactions	none	none	none		S x P	S x P	none	

For a given area, growth measure, and environmental parameter, different superscripts indicate significantly different ($P < 0.05$) magnitudes of growth. An absence of superscripts indicates no significant differences in growth. Standard errors are given in parentheses.
n = number of observations.

can be attributed to the warmer climate and nutrient richer forest floors at Cedar Creek *Thuja* grows better in the warmer portions of the Coastal Western Hemlock biogeoclimatic zone in southwestern B.C. (Kayahara et al. 1997) and the Cedar Creek Mormoder forest floors have lower C/N ratios and greater mineralizable N contents than the Leptomoder forest floors at Eastcap Creek (Fons and Klinka 1998). The mineral soils at both sites are poorer growing sites for *Thuja* than burned or undisturbed forest floors. This may be due to poorer nutrition or water supply in the mineral soil. Regardless of the reason, an increase in growth (from mineral soil to forest floor) is likely to be enhanced in the better growing environment of Cedar Creek.

Trends in seedling growth with light were quite clear and identical at both study sites. Seedling growth was better in clearcuts than in forests. The same result has been found for *Thuja* seedlings planted in the study sites (Wang et al. 1994). Adams and Mahoney (1991) found that naturally regenerated *Thuja* seedlings in Idaho grew best in partial shade and that growth was reduced more by below-ground competition than by competition for light. Competing vegetation was removed from all plots in the present study on all seedling counting occasions during the growing season. This was necessary primarily in the clearcuts where herb and shrub species regenerated prolifically. The roots of trees and shrubs, however, would have been present to a greater extent in the forests than in the clearcuts. The competition environments of the study plots were not quantified. Consequently, it is unclear whether competition would have been greater in the forests or the clearcuts. However, seedlings grew better in mineral soil seedbeds in the clearcuts than in the forests. In these seedbeds below-ground competition would have been minimal as many roots were destroyed when the seedbeds were prepared. Furthermore, after 3 years, 9 plots had more than 10 *Thuja* seedlings present. Two of these plots contained 57 and 59 seedlings, respectively. Although there were no visible indications that competition between seedlings in these plots had affected seedling growth, the ANOVA was rerun excluding data from these 9 plots. The results were still identical to those presented in Table 2. Consequently, although we have not been able to definitely exclude the effects of below-ground competition, our data and

observations suggest that light had an important influence on *Thuja* seedling growth in our study area, with greater growth in the higher light levels in clearcuts rather than in forests.

Predation also appeared to influence growth with greater growth in plots where vertebrate predators were excluded (Table 2). However, seedbed interacted with predation at Cedar Creek such that basal diameter differences were statistically significant only on mineral soil seedbed plots. *Thuja* seedlings in plots without predator exclusion screens would have been available to herbivores. Deer, which are present in the study area, are known to browse *Thuja* seedlings heavily (Minore 1983). Curran and Dunsworth (1988) considered that damage from browsing may be the most important stand establishment problem for *Thuja* in coastal British Columbia. Thus, it is likely that browsing on the *Thuja* seedlings in plots without predator exclusion screens retarded aboveground seedling growth in relation to that in plots surrounded by screens. It is unclear why differences were statistically significant only on mineral soil seedbeds at Cedar Creek, unless this is partly an artifact caused by the small sample size (n=6) on forest floor seedbeds, and partly due to the greater visibility of seedlings on the mineral soil seedbeds.

Conclusions

We conclude that the relative lack of *Thuja* seedlings in the forests of the study area was not due to a lack of viable seeds. Although a lack of suitable seedbeds and the presence of the forest canopy reduces the number of seedlings in undisturbed old growth forests, this number should still be substantial. The observed relative lack of *Thuja* seedlings must result from other factors, such as pre-logging wildlife browsing or understory plant competition, which were not investigated in the present study. Investigation of these factors is warranted if the relative lack of *Thuja* regeneration is to be explained.

The results of the present study also support the hypothesis of Daniels et al. (1995) that regeneration peaks of *Thuja* in the study area forests occurred following fire or windthrow events. Daniels et al. (1995) were not able to discount the influence of a variable climate in explaining *Thuja* regeneration peaks. The more abundant germinants in the experimental plots, and *Thuja* regeneration in the warmer Cedar Creek forest than in the cooler Eastcap Creek forest is also consistent with this. However, the low number of germinants and poor survival of seedlings on forest floor seedbeds even in the warmer Cedar Creek forest suggest that *Thuja* regeneration is more responsive to seedbed conditions than to small changes in temperature. However, the effects of major changes in temperature (i.e., increases of >5°C in annual or growing season mean daily temperature) are still uncertain. Climate is certain to influence *Thuja* regeneration indirectly through its influence on fire incidence. Warmer, drier climates will increase fire incidence and lead to greater *Thuja* regeneration, unless the fires are so severe as to kill the mature *Thuja* trees over large areas and thus eliminate the *Thuja* seed source.

Acknowledgements

E. Kastner, R. McDowell, D. New, L. Pelles, J. Olinek, A. Pölchen and P. Wycherley assisted in the field and the laboratory, as did P. Olanski, who also assisted with data analysis. The staff of the Greater Vancouver Water District assisted in providing materials and supplies, and with burning operations. Financial support was provided by the Vancouver Forest Region of the B.C. Ministry of Forests.

Literature Cited

Adams, D. L., and R. L. Mahoney. 1991. Effects of shade and competing vegetation on growth of western redcedar regeneration. W. J. Appl. For. 6: 21-22.

Canada Soil Survey Committee. 1987. The Canadian system of soil classification. 2nd ed. Agric. Can. Publ. No. 1646, 164 pp.

Carter, R. E., and K. Klinka. 1992. Variation in shade tolerance of Douglas-fir, western hemlock, and western red cedar in coastal British Columbia. Forest Ecol. Manage. 55: 87-105.

Curran, M. P., and B. G. Dunsworth. 1988. Coastal western redcedar regeneration: problems and potentials. *In* N. J. Smith (Compiler), Western red cedar—does it have a future? Conference Proceedings. Faculty of Forestry, University of B.C., Vancouver, B.C. Pp. 20-32.

Daniels, L. D., P. L. Marshall, R. E. Carter, and K. Klinka. 1995. Age structure of *Thuja plicata* in the tree layer of old-growth stands near Vancouver, British Columbia. Northwest Sci. 69: 175-183.

Eis, S. 1962. Statistical analysis of several methods for estimation of forest habitats and tree growth near Vancouver, B.C. Forestry Bulletin No. 4. Faculty of Forestry, University of British Columbia, Vancouver, B.C.

Ferguson, D. E. 1994. Natural regeneration following timber harvest in Interior cedar - hemlock - white pine forests. *In* D. M. Baumgartner, J. E. Lotan, and J. R. Tonn (eds.) Interior - cedar hemlock - white pine forests: ecology and management Conf. Proc. Cooperative Extension, Washington State University, Pullman Wa. Pp. 239-247.

Fons, J. and K. Klinka. 1998. Chemical and biotic properties and temporal variation of moder humus forms in the rain forest near Vancouver, British Columbia. Can. J. For. Res. 28: in press.

Gashwiler, J. S. 1971. Emergence and mortality of Douglas-fir, western hemlock, and western redcedar seedlings. Forest Sci. 17: 231-237.

Haig, I. T., K. P. Davis, and R. H. Weidman. 1941. Natural regeneration in the western white pine type. U.S.D.A. For. Serv. Tech. Bull. 767, Northern Rocky Mountain For. Ran. Exp. Sta., Missoula, Montana, 99 pp.

Harmon, J. M., and J. F. Franklin. 1995. Seed rain and seed bank of third- and fifth- order streams on the western slope of the Cascade Range. Res. Pap. PNW-RP480. U.S.D.A. Forest Service. Pac. Northwest Res. Stn., Portand, Or. 27 p.

Kayahara, G.J., K. Klinka, and A. C. Schroff. 1997. The relationship of site index to synoptic estimates of soil moisture and nutrients for western redcedar (*Thuja plicata*) in southern coastal British Columbia. Northwest Sci. 71:167-173.

Klinka, K., J. Pojar, and D. V. Meidinger. 1991. Revision of biogeoclimatic units of coastal British Columbia. Northwest Sci. 65: 32-47.

Krajina, V. J. 1969. Ecology of forest trees in British Columbia. Ecology of Western North America 2 (1): 1-147, Department of Botany, University of B. C., Vancouver, B.C.

Krajina, V. J., K. Klinka, and J. Worrall. 1982. Distribution and ecological characteristics of trees and shrubs of British Columbia. Faculty of Forestry, University of British Columbia, Vancouver, B.C. 131 p.

Li, X.J., P.J. Burton, and C.L. Leadem. 1994. Interactive effects of light and stratification on the germination of some British Columbia conifers. Can. J. Bot. 72: 1635-1646.

Received 3 December 1997
Accepted 15 May 1998

McGee, A., and M. C. Feller. 1993. Seed banks of forested and disturbed soils in southwestern British Columbia. Can. J. Bot. 71: 1574-1583.

Minore, D. 1983. Western redcedar—a literature review. Gen. Tech. Rep. PNW-150. U.S.D.A. Forest Service Pac. Northwest For. Ran. Exp. Stn., Portland, Or. 70 p.

_____. 1990. *Thuja plicata* Donn ex D. Don. *In* R. M. Burns, and B. H. Honkala (eds.) Agriculture Handbook: 654, U.S.D.A. Forest Service, Washington, D. C. pp. 590-600.

Parker, T. 1986. Ecology of western redcedar groves. Ph.D. Thesis, University of Idaho, Moscow, Idaho.

Parker, T., and F. D. Johnson. 1994. Cedar groves: the ultimate old growth. *In* D. M. Baumgartner, J. E. Lotan, and J. R. Tonn. (eds.)Interior Cedar - hemlock - white pine forests: ecology and management Conf. Proc. Cooperative Extension, Washington State University, Pullman, Wa. Pp. 53-55.

Soil Survey Staff. 1975. Soil taxonomy. U.S. Dep. Agric. Handbook 436, 503 pp.

Song, X. 1997. Relationships between coarse woody debris and understory vegetation in six forest ecosystems in British Columbia. M.S. Thesis, Faculty of Forestry, University of B.C., Vancouver, B.C. 109 p.

Soos, J., and Walters, J. 1963. Some factors affecting the mortality of western hemlock and western red cedar germinates and seedlings. University of B.C. Fac. For. Res. Pap. 56.

Wang, G. G., H. Qiang, and K. Klinka. 1994. Growth of *Thuja plicata* seedlings along a light gradient. Can. J. Bot. 72: 1749-1757.

Wilkinson, L. 1986. SYSTAT. The system for statistics. SYSTAT Inc., Evanston, Illinois.

Yearsley, H. K. 1993. Forest floor seed banks and their response to slashburning in some forest ecosystems in south central British Columbia. M. Sc. Thesis, Faculty of Forestry, University of B. C., Vancouver, B. C. 136 p.

Gregory D. Hayward, Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming 82071

and

George C. Iverson, Alaska Region, U.S.D.A. Forest Service, P. O. Box 21628, Juneau, Alaska 99802-1628

Long-Term Trend In Marbled Murrelets In Southeast Alaska Based On Christmas Bird Counts

Abstract

A significant proportion of marbled murrelets (*Brachyramphus marmoratus*) occur in Southeast Alaska. We examined long-term trends in marbled murrelet abundance in this region by analyzing published Christmas Bird Counts (CBC) for 7 sites from 1971 to 1993. We analyzed records of murrelet counts and counts standardized by effort. Murrelet counts were highly variable, in particular, most sites recorded one or a few unusually high counts during the time series. Our exploration of trend using a battery of statistical analyses failed to provide evidence for a decline in marbled murrelets across the region for the period 1971-1993. In general, there was high concordance among sites when counts occurred in the same year (e.g. Kendall's $W = 0.822$, $P = 0.0025$ among 5 sites) which supports our argument that trends in murrelet abundance should be examined for the region as a whole rather than focusing on individual sites. Although our analyses provide little evidence for a sustained decline in marbled murrelets in Southeast Alaska, we suggest that our failure to detect a decline does not indicate that a decline has not occurred, only that CBC data does not support such a conclusion.

Introduction

Marbled murrelets (*Brachyramphus marmoratus*) occur in coastal marine environments from central California to the Bering Sea and nest in coastal forests or on the ground in treeless regions. Compared to other seabirds in the region, the demography of this small cryptic seabird suggests that marbled murrelets may be particularly sensitive to environmental changes which influence adult survival (Ralph et al. 1995:13). Whereas some seabirds appear to rebound rapidly from natural (e.g. Harris and Wanless 1984) and anthropogenic catastrophes (e.g. Evans et al. 1993, Wiens et al. 1996, Day et al. 1997), other species, especially those with single egg clutches such as the marbled murrelet, may not have this capacity for rapid recovery (Ralph et al. 1995). Relatively small, long-term reductions in productivity and survival may jeopardize persistence of marbled murrelets to a greater extent than other alcids within its range (Ralph et al. 1995).

Recognized threats to marbled murrelet populations include natural reductions in prey fish due to long-term cyclic changes in sea water temperature, mortality from gill-net fishing, chronic marine oil pollution, large oil spills, and reduction in the geographic extent of coastal old-growth forests used for nesting (Piatt and Naslund 1995). Whereas marbled murrelets have endured natural fluctuations in the marine environment, the intensity of anthropogenic threats may be increasing (Carter et al. 1995, Carter and Kuletz 1995). In particular, the extent of old-growth forests used for nesting has declined significantly in Southeast Alaska during the past century (U.S.D.A. Forest Service 1991, Perry 1995). For instance, on the Tongass National Forest and surrounding forest lands in Southeast Alaska, approximately 384,000 ha, or about 17% of the "productive old forest" has been harvested since the early 1900's. Therefore, efforts to examine trends in regional populations of murrelets are becoming increasingly important in assessing the impact of human activities.

Concerns for the conservation status of marbled murrelets in coastal Washington, Oregon, and California led the U.S. Fish and Wildlife Service to list the species as threatened under the Endangered Species Act in September, 1992 (U.S. Fish and Wildlife Service 1992). The marbled murrelet population in North America was estimated to be on the order of 300,000 individuals with approximately 280,000 in Alaska (Ralph et al. 1995, Piatt and Naslund 1995). Recent comprehensive surveys place the estimate of all *Brachyramphus* near 687,000 in Southeast Alaska with a majority being marbled murrelets (Agler et al. 1998). An in-depth assessment of marbled murrelet conservation

© 1998 by the Northwest Scientific Association. All rights reserved.

status in 1995 suggested that "available evidence indicates that the population of murrelets has declined over most of its range" (Ralph et al. 1995:17). More important, Piatt and Naslund (1995:294) stated that "populations in Alaska have apparently declined by more than 50 percent over the last 20 years." Their inference concerning trends in Alaska was based in part on examination of 20 years (1972-1991) of Christmas Bird Counts (CBC) from five of the 13 available CBC sites extending from the Northern Gulf of Alaska south to Sitka.

Based on this estimate of population decline and concern over loss of old-growth forest in Southeast Alaska, we sought to determine the long-term trend in murrelet populations for a more limited portion of Alaska but that portion supporting much of the species. We relied on Christmas Bird Counts as the most complete, long-term record of population trend. Since the early 1970's, volunteers recorded marbled murrelet numbers at seven locations in Southeast Alaska as part of the national Christmas Bird Count. These counts represent the longest time series available to examine potential changes in populations of this seabird in the region. Furthermore, a majority of the evidence leading to the inference by Piatt and Naslund (1995) that murrelets had declined by 50% in Alaska came from CBC data analyzed from a limited number of sites dispersed along the Alaska coast.

For a variety of reasons, counts from the CBC represent a very imperfect index to population trends (Bock and Root 1981). Some problems particular to marbled murrelets include the small marine area sampled relative to the distribution of the species, the clumped and variable distribution of murrelets during winter, and the relatively low number of sightings during counts relative to the total population. Winter distribution of marbled murrelets in Alaska is poorly understood (Piatt and Naslund 1995). In British Columbia, murrelets tend to occupy nearshore waters in protected areas during winter (Burger 1995) which would facilitate CBC trend counts. Christmas Bird Count data are an inappropriate substitute for, long-term, rigorously designed, local surveys (Bock and Root 1981) and must be regarded with skepticism compared to controlled censuses. However, as noted by Butcher (1990), other sources of bird population information frequently correlate with trends illustrated by CBC data.

As with any index, the degree to which survey conditions are controlled across years will strongly influence the performance of CBC in revealing true population patterns. Christmas Bird Counts are not as controlled as some scientific surveys (Bock and Root 1981, Butcher 1990). Therefore patterns observed from individual sites, if considered in isolation, are as likely to result from bias in the index as from pattern in bird population numbers. If regional effects are driving population trends, however, concordance among many sites from a region can provide evidence that bird population changes, rather than changes in the index, are responsible for observed patterns. Furthermore, because marbled murrelets in Southeast Alaska represent a regional breeding population (Piatt and Naslund 1995), combined counts from several sites throughout the region are most likely to reflect true population changes. Therefore, we examined murrelet population trend by focusing on all CBC data from Southeast Alaska. It should be emphasized that we focused on CBC counts because they represent the only long-term data for this population and the counts were used as the primary empirical basis for the estimate of a 50% decline in murrelets in Alaska.

Methods

We examined CBC data from 1971 to 1993 for seven sites in Southeast Alaska: Craig, Glacier Bay, Haines, Juneau, Ketchikan, Mitkof, and Sitka. These sites represent all the CBC sites from Southeast Alaska with records of marbled murrelets and overlaps with the group of CBC sites sampled by Piatt and Naslund (1995). Both Piatt and Naslund (1995) and we sampled Sitka, Juneau, and Glacier Bay, however we also examined the other 4 CBC sites from Southeast Alaska. Piatt and Naslund (1995) included Cordova and Kodiak Island, two sites far to the north, in their sample. For our analysis we focus on data published in *American Birds* as of the date we initiated this analysis (we include some analysis of counts from 1994-1996, however, to determine whether patterns observed through 1993 continued). The number of years surveyed, the first year surveyed, and the number of missing years after initiation varied among sites (Table 1). We examined both counts of murrelets and counts standardized by effort (murrelet count divided by total party-hours). Bock and Root (1981) suggest that effort is only

TABLE 1. Counts of marbled murrelets, and counts standardized by effort (party hours), from 1971-1996 for seven sites in

Site	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983
Murrelet counts													
Craig										0		0	
Glacier Bay	100	14		44	119	72		339		12	3	11	56
Haines						61	7		0	0	0	0	0
Juneau	102						35	148	19	5	5	53	24
Ketchikan					1								
Mitkof		0											
Sitka					1	2	141	339	8			25	31
Murrelet counts standardized by effort													
Craig										0		0	
Glacier Bay	3.57	0.41		1.38	2.64	2.12		7.88		1.09	0.13	0.32	2.33
Haines						3.05	0.23		0	0	0	0	0
Juneau	2.08						0.92	5.48	0.46	0.26	0.25	2.52	0.69
Ketchikan					0.03								
Mitkof		0											
Sitka					0.08	0.12	3.53	11.3	0.13			0.51	1.41

poorly related with numbers of birds counted for certain species because some species are easily observed. It is unknown whether CBC counts of murrelets depend strongly on effort (number of party hours). Therefore, we looked at both the raw counts and the standardized counts which we call count/effort data.

Approach

We examined data by looking both at patterns of counts from individual CBC sites and combined the data from several sites. Our goal in the analysis centered not on determining population trend at particular CBC survey locales, but determining whether the CBC surveys for Southeast Alaska together suggest a trend in marbled murrelet population size in the region; we suggest that murrelets throughout Southeast Alaska represent the biological population of interest. Therefore, a variety of statistical approaches were employed to explore common patterns.

Because trend data can provide input to conservation programs for the marbled murrelet we paid particular attention to the consequences of Type II errors (failure to detect a downward trend). To increase the power of the test, in some analyses (Spearman rank correlation) we employed a one-tailed test explicitly examining hypotheses concerning downward trends. To further increase the chance of detecting a downward trend we employed a battery of statistical procedures, each with slightly different emphases and assumptions (Table 2). For all tests we paid particular attention to assumptions of the test prior to conducting any analysis. Here we concentrate on those tests least influenced by the extreme counts (nonparametric tests) although as indicated in Table 2, the results of all analyses lead to similar conclusions. The statistical details of the tests reported here are described below. Those who find statistical details tedious may wish to move directly to the results.

Individual Sites

Normal, least-squares regression is sensitive to extreme observations, especially at the ends of the gradient sampled for the independent variable (Belsey et al. 1980). A review of CBC data for the seven Southeast Alaska sites shows that at almost every site, the count for one year exceeded all others by a factor of two and up to 10 (Table 1). Given this and the potential sources of variation in CBC data due to observers and other conditions not related to murrelet abundance, we examined the pattern of yearly counts using a variety of nonparametric methods.

southeast Alaska.

1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996
3		18			1	13	26	0	8	0	0	0
152		207	16	1		163			1478	474	1001	58
0	0	0	0	0	37	0	3	2	4	0	11	29
22	23	21	39	31	44	25	24	63	67	40	96	24
					38	56	56	693	48	42	105	31
				17	52	53	8	24	54	92	75	40
4	1	16	6	3	3	2	1	13	26	10	77	76
0.38		2			0.03	0.34	1.24	0	0.33	0	0	0
4.47		7.39	0.38	0.02		4.79			54.74	17.56	29.44	2.0
0	0	0	0	0	1.42	0	0.2	0.07	0.19	0	0.41	0.87
0.58	0.48	0.88	1.63	0.74	0.92	0.47	0.65	1.58	1.56	0.74	1.45	0.46
					1.19	0.97	1.06	12.4	1.0	0.73	2.10	0.76
				2.13	5.20	2.41	0.38	0.96	6.75	6.13	5.00	2.58
0.13	0.02	0.64	0.20	0.10	0.10	0.06	0.01	0.37	0.63	0.22	1.44	1.67

TABLE 2. Overview of analyses of marbled murrelet population trend as indicated by CBC counts at seven sites in Southeast Alaska. Each test was run for each of the seven sites or a combination of sites. Results summarize the broad pattern suggested by the group of analyses. Details are presented in methods and results.

Test	Why performed	Results
Runs tests	Search for evidence of a nonrandom pattern.	No evidence for patterns (Table 3)
Regression using rank transformed data	Search for downward trend w/ test not sensitive to extreme values.	Little evidence for downward trend (1 of 14 P-values < 0.10) (Table 4)
Spearman Rank Correlation	Search for downward trend w/ alternative test not sensitive to extreme values.	Little evidence for downward trend (2 of 14 P-values < 0.10) (Table 4)
Normal least-squares regression	Search for downward trend employing power of normal theory	No evidence for downward trend (Unpublished results)
Kendall's W	Examine degree of concordance among 7 CBC sites — do increases and decreases correspond across sites, within years.	Strong evidence for concordance among CBC sites (5 of 7 P-values < 0.01) (Table 5)
Tests on 'collapsed' data sets	Search for downward trend based on summed counts across all CBC sites using tests described above	No evidence for downward trend (Table 6 and unpublished results)

We first employed a series of runs tests (Daniel 1978) for evidence of a trend. Rejection of the null hypothesis—departures from the median over time are random—indicates a trend but does not suggest the particular nonrandom pattern.

We further examined the relationship between murrelet counts (and count/effort data) and year of census using Spearman rank correlation (Daniel 1978). A significant statistic would suggest murrelet numbers were falling during the period of surveys (one-tailed test).

We also examined several least-squares regression models but here concentrate on models of rank transformed data (Conover and Iman 1981); an approach less influenced by outliers. We tested whether the slope of the function relating murrelet abundance to year was significantly different from zero.

Combining CBC Sites

We employed two basic approaches to examine the pattern in CBC counts across sites. First, regardless of whether or not CBC counts suggested a long-term decline in murrelet numbers throughout the region, we were interested in whether there was concordance among sites in murrelet abundance (i.e., did annual counts increase and decrease together across the region?) . For this analysis we employed Kendall's W or Coefficient of Concordance (Daniel 1978). We examined Kendall's W for both murrelet counts and count/effort data. This test is analogous to Spearman rank correlation but tests for association among many sets of rankings, rather than just two.

Missing data within the time series for individual sites posed a problem (see Table 1). The time series examined using Kendall's W was determined by the number of years in which all sites had data; a missing value for any one site rendered a particular year missing for the analysis. Therefore we looked at 3 groupings of sites; 1) Glacier Bay, Juneau and Haines, n=10; 2) Glacier Bay, Juneau, Craig and Haines, n=6; 3) Glacier Bay, Juneau, Craig, Haines and Sitka, n=5. Only 2 years contain data on all seven sites (note that Table 1 includes data from 3 years beyond the years analyzed here).

To determine whether CBC sites, as a group, suggested a long-term decline in murrelet numbers, we combined the counts and count/effort across sites in two ways, using rank transformed data and using the untransformed data.

In order to combine sites it was necessary to either fill in years with missing data or eliminate years in which one of the sites being 'summed' lacked data. To maintain the benefits of a long, continuous time series we chose to fill in missing cells. We filled in missing cells only in cases lacking one or two years in succession for a site. If more than two cells where missing from a time series, the cells retained missing values. To fill in missing values, we applied the mean of the neighboring years to the missing year. When more than 2 years were missing from a time series, the CBC site could not be used to produce a summed score for the region based on those years. Relative to the number of years (time line), this procedure would have injected minimal dependence among years into the data. For instance nine of 68 cells were estimated for a 17-year trend examining combined data from four bays. The effect is also reduced because we used a ranking procedure to analyze the data.

After filling in missing cells, we calculated the rank score, within sites, for all CBC sites. We summed the rank scores within years for several combinations of sites. Our goal was a long time series that lumped as many sites as possible. We produced four groupings of sites: one grouping of four sites (Glacier Bay, Haines, Juneau, and Sitka) spanning 17 years; one grouping of three sites (Glacier Bay, Haines, and Sitka) spanning 18 years, and one grouping of two sites (Glacier Bay and Sitka) spanning 19 years.

We also summed the raw counts across these same groups of CBC sites. This produced collapsed data sets with similar structure as the collapsed, rank data but containing the actual counts (or count/effort data).

Results

Counts of murrelets showed high variability (Table 1). At most sites, counts in one or two years exceeded all other years by a factor of two. At Glacier Bay, the count in 1993, 1478 marbled murrelets, exceeded the next highest count (339 in 1978) by over a factor of four. At Haines, no marbled murrelets were reported in 11 of the 17 years but 61 and 37 murrelets were counted in 1976 and 1989. The most extreme variation occurred in the short time series reported for Ketchikan (n=6); volunteers counted 693 murrelets in 1992 while the next highest count was 56 in both 1990 and 1991.

No consistent trend in murrelet abundance was apparent at individual sites or across the region after examining data from multiple sites (Table 2). The pattern of no trend was robust across a battery of statistical tests. Below we describe the results in detail.

Individual Sites

The series of marbled murrelet counts at seven CBC sites showed no strong evidence for a nonrandom pattern over the period of record (Table 3). Runs tests tended to produce very high *P*-values suggesting no evidence for pattern in the time series.

Based on rank-transformed data (counts and count/effort), only a single linear regression model had a *P*-value less than 0.10 for the test of a slope different from zero (Table 4). All models with *P*-values less than 0.30 showed positive slopes suggesting, if anything, trends of increasing counts.

Spearman rank correlation (on counts and count/effort data) generally corroborated the patterns observed in the regression models examining rank transformed data (Table 4). Spearman rank correlation, however, suggested some relationship between counts and year. Ketchikan and Mitkof both had *P*-values less than 0.10; in both cases the relationship was positive but the counts only represent trends for the late 1980's and early 1990's (Table 1). Overall the results did not suggest a common trend for the region.

TABLE 3. Examination of pattern in CBC counts for marbled murrelets in Southeast Alaska. Runs test examining hypothesis that pattern of counts over time displays a departure from the median or mean value which is random. A significant test suggests a nonrandom pattern. Tests here examine raw count data and employ the SPSS exact module to calculate the *P*-value.

Location	No. of years	Runs test value	Exact *P*-value
Median			
Craig	9	3	0.762
Glacier Bay	16	64	0.429
Haines	17	could not be run because of # of zeros	
Juneau	18	28	0.218
Ketchikan	6	52	0.600
Mitkof	7	24	0.999
Sitka	17	6	0.129
Mean			
Craig	9	7.666	0.286
Glacier Bay	16	174.187	0.999
Haines	17	6.706	0.101
Juneau	18	41.666	0.999
Ketchikan	6	148.666	0.999
Mitkof	7	29.714	0.999
Sitka	17	36.588	0.125

TABLE 4. Trend in marbled murrelet abundance at seven CBC sites in Southeast Alaska. Analyses include regression based on ranks and Spearman Rank Correlation. For both models we examine rank counts and rank count/effort. Values reported are the number of years in time series, the regression coefficient (ß), significance of the regression model, Spearman rank correlation, and significance of the correlation.

Location	No. of years	Coef. for Year	*P*-value	Spearman Rank Corr.	*P*-value
Counts					
Craig	9	0.139	0.534	0.389	0.150
Glacier Bay	16	0.120	0.539	0.171	0.264
Haines	17	0.048	0.825	0.106	0.343
Juneau	18	-0.062	0.785	0.119	0.318
Ketchikan	6	0.179	0.171	0.637	0.087
Mitkof	7	0.183	0.145	0.607	0.074
Sitka	17	-0.205	0.361	-0.114	0.331
Count/effort					
Craig	9	0.343	0.099	0.186	0.315
Glacier Bay	16	-0.016	0.933	0.141	0.301
Haines	17	-0.218	0.381	0.100	0.351
Juneau	18	0.170	0.453	-0.009	0.485
Ketchikan	6	0.152	0.261	0.428	0.198
Mitkof	7	0.132	0.304	0.428	0.169
Sitka	17	0.284	0.197	-0.236	0.181

Trends After Combining CBC Sites

In general, murrelet counts (and count/effort data) throughout Southeast Alaska appear to vary in concordance with one another. We found strong evidence suggesting that CBC records for murrelets varied similarly throughout Southeast Alaska (Table 5).

Given the degree of concordance among CBC sites across Southeast Alaska, we examined the trend in CBC records for the region as a whole. Regression models based on sums of rank transformed count and count/effort data produced no evidence for a temporal trend in murrelet observations over the period of CBCs (Table 6). Spearman rank correlations examining data from all CBCs for Southeast Alaska also produced little evidence for long-term downward trend in counts or count/effort data (Table 6).

Discussion

The pattern of counts and counts standardized by effort (count/effort) from seven CBC sites in Southeast Alaska provide no evidence for a broad, sustained decline in marbled murrelets across the region for 1971-1993. Our failure to detect a decline does not indicate that a decline has not occurred. Power analyses are not available for the nonparametric tests examined here. By employing one-tailed tests, examining long time series, and using a battery of statistical analyses we sought to increase the power of our analyses to detect downward trends. Variability in counts, however, reduces power and these analyses examined data with high variability in year-to-year counts.

The most striking feature of the murrelet counts concerns the presence of one or a few unusually

TABLE 5. Concordance among CBC sites throughout Southeast Alaska as indicated by Kendall's W. Statistic indicates the degree to which values at several sites vary together; the degree to which they rise and fall as a unit. Number of years refers to the sample size for individual tests. Statistic tests the hypothesis that concordance = 0; rejection of the null hypothesis suggests evidence for concordance.

Locations	No. of years	Kendall's W	*P*-value
Counts			
Glacier Bay, Haines, Juneau	10	0.760	0.0005
Glacier Bay, Haines, Juneau, Craig	6	0.919	0.0009
Glacier Bay, Haines, Juneau, Craig, Sitka	5	0.822	0.0025
Count/effort			
Glacier Bay, Haines, Juneau	10	0.760	0.0005
Glacier Bay, Haines, Juneau, Craig	6	0.839	0.0017
Glacier Bay, Haines, Juneau, Craig, Sitka	5	0.749	0.0047

TABLE 6. Trend in marbled murrelets from CBC counts throughout southeast Alaska based on linear regression models and Spearman rank correlation of *summed ranks*. Location refers to the group of CBC sites summed to form the dependent variable. Values reported include the number of years in the trend, regression coefficient (ß), significance of the regression model for ranks, Spearman rank correlation, and significance of the correlation.

Locations	No. of years	Regression Coef.	*P*-value	Spearman Rank Corr.	*P*-value
Counts					
Glacier Bay, Haines, Juneau, and Sitka	17	0.240	0.755	0.124	0.318
Glacier Bay, Haines, and Sitka	18	0.026	0.961	0.013	0.479
Glacier Bay and Sitka	19	0.138	0.732	0.096	0.348
Count/effort					
Glacier Bay, Haines, Juneau, and Sitka	17	0.035	0.944	0.094	0.359
Glacier Bay, Haines, and Sitka	18	-0.223	0.576	-0.126	0.309
Glacier Bay and Sitka	19	-0.059	0.843	0.017	0.473

high counts at each site; high counts are found in both the first and second half of the time series in almost equal proportions. High counts likely arise because CBC counts in Southeast Alaska sample a very small portion of the marine environment occupied by murrelets. The total count from all sites in any one year represented less than 1 percent of the estimated breeding population of the region. Murrelet numbers in small areas show variation with weather, tide, time of day, and local food availability (e.g. Carter and Sealy 1990).

The variability in counts at individual sites lead to difficulties examining murrelet trend for individual sites. However, we are most interested in using CBC data to uncover long-term trends on a regional basis as suggested by Butcher (1990). In this light, it seems reasonable to argue that the pattern exhibited by all seven CBC sites, taken as a unit, may represent an index to wintering murrelet abundance in the broad region of Southeast Alaska. Our analysis suggested concordance among sites. Concordance among sites supports an approach which examines the broad pattern of population change among the sites as a unit.

In general, our analysis of available CBC data provides little evidence for either increasing or decreasing trends in marbled murrelets for Southeast Alaska over the past couple decades. Our analysis is not alone in failing to detect the marked recent decline in murrelets noted by Piatt and Naslund (1995). Murphy et al. (1997: Table 1) examined counts of murrelets in selected portions of Prince William Sound comparing surveys in 1984/85 with 1989, 1990, and 1991. Their results suggest no change (1984 vs. 1989 and 1984 vs. 1990) or an increase in murrelet numbers (1984 vs. 1991). Murphy et al. (1997) did note the low power of their tests for the first two comparisons. These results are especially interesting given the documented mortality of murrelets in Prince William Sound as a result of the *Exxon Valdez* oil spill in March of 1989 (Piatt et al. 1990, Day et al. 1997). In contrast to the results of Murphy et al. (1997), Klosiewski and Laing (1994) report declining murrelet numbers in Prince William Sound between 1972 and 1991. Klosiewski and Laing (1994) and Murphy et al. (1997) used different methods and sampled different portions of Prince William Sound.

The mixed evidence for declining populations is interesting considering the negative trend in certain resources important to murrelets. In the Pacific Northwest, remaining murrelet populations appear to be closely associated with coastal waters adjacent to late-successional forest (Ralph et al. 1995). Harvest of productive virgin forest in Southeast Alaska has removed 182,250 ha of old forest (or about 8% of the commercially valuable timber land) on the Tongass National Forest since 1909 (U.S.D.A. Forest Service 1991); this land area does not include the significant harvest of old forest from non-federal land. In addition to the loss of potential nesting habitat, changes in the marine ecosystem in the Gulf of Alaska are purported to have reduced availability and biomass of important prey fish (Piatt and Anderson in press, as cited by Piatt and Naslund 1995). If marbled murrelet populations are not declining in response to these changes, the abundance of this seabird may currently be determined by other factors in Southeast Alaska.

Analyses of CBC data should be viewed as a preliminary examination of population patterns when more rigorous survey information is lacking. Our analysis does not assess potential bias associated with these data resulting from changes in methods, survey protocol, or the geographic relationship between CBC sites and murrelet concentrations in Southeast Alaska. Sites chosen for CBCs may or may not survey geographic areas important to murrelet trends in Southeast Alaska. Furthermore, there may be a substantial lag between decline in reproduction and numbers of adult birds observed during winter surveys. Therefore, strong conclusions concerning murrelet trend in Southeast Alaska cannot be established based on these data. Marbled murrelet populations may indeed be in peril within Southeast Alaska, but no such trend can be detected with the only available, long-term data using a variety of analyses.

Decisions regarding conservation of murrelets in Southeast Alaska require some indication of population trends in the region. Our conclusion (absence of strong evidence for a sustained decline in marbled murrelets), drawn from seven sites in Southeast Alaska differ from those of Piatt and Naslund (1995) who examined five sites extending from the Northern Gulf of Alaska south to Sitka. Reasons for these differences are not clear but may be related to differences in geographic areas examined, problems in data analysis and interpretation, or unrecognized aspects of murrelet biology and movements. The disparity between our conclusions and those reached by Piatt and Naslund (1995) invites explanation.

Piatt and Naslund (1995) examined CBC data from five of the 13 available CBC sites throughout coastal Alaska. Sites they examined include Cordova and Kodiak Island; coastal areas which represent two relatively independent breeding areas hundreds of kilometers north of the breeding unit in the Alexander Archipelago sampled by their other three sites (Piatt and Naslund 1995:286). Therefore, their choice of sites has a high probability of mixing counts from populations or subpopulations that may be influenced by very different factors. We chose to examine all available sites from one region, Southeast Alaska, to avoid this potential problem. Furthermore, their sample also included only the northern subset of CBC sites from Southeast Alaska. The limited sample Piatt and Naslund (1995) examined from Southeast Alaska could lead to different observed patterns in abundance than those we detected in our analysis. Our analysis more adequately sampled the geographic extent of the population in Southeast Alaska and avoided the potential problems of mixing samples from two, geographically distinct groups of murrelets.

Piatt and Naslund's (1995:293) conclusions are further compromised by problems in data analysis and interpretation. Among other problems, they interpreted trends after they "smoothed [*summed counts*] by taking 5-year running averages of the annual data" (italic ours). Trend analysis assumes independent observations and employing a moving average explicitly creates dependence among observations (Kendall 1973). Interannual variation in murrelet abundance is removed by this approach, and high or low counts from a single year become part of the apparent pattern for four more years. Based on their report, Piatt and Naslund reached their conclusion regarding a "steady decline in abundance of about 50 percent" based on visual inspection of a plot of the smoothed data (see Figure 7 in Piatt and Naslund 1995:294). However, visual inspection of the plot shows that plotted values from 1974 to 1979 changed little. In the next year, though, the plotted value dropped by almost 50 percent and then remained about the same for the next 10 years. This step change in the plotted values between 1979 and 1980 is the most striking feature of their analysis, rather than a "steady decline in abundance."

An examination of potential environmental explanations for the differing conclusions of our studies may be unwarranted given the potential problems with the analysis presented by Piatt and Naslund (1995). Further examination of the demography of marbled murrelets will be necessary to determine trends for this species in Southeast Alaska. Finally, informed conservation decisions in the future will depend on a strong, long-term monitoring program, not linked to CBC counts, to assess trend in murrelet abundance.

Epilogue

Our analysis was conducted prior to formal publication of the results reported by Piatt and Naslund (1995); when we began, data was available through 1993. Through our analysis, we sought to compare trends for murrelets in the Alexander Archipelago with conclusions reached in the murrelet assessment (Ralph et al. 1995). Because of the variety of statistical approach we used to examine the data, our analyses included over 100 statistical tests. Therefore, we have not run our full analyses with counts that now exist in reports for 1994-1996. We have examined the recent data, however, to determine whether the new information would likely change the conclusions reached from our analysis.

Counts from all 7 bays in 1994, 1995 and 1996 (see Table 1) are either within the 95 percent bound on the mean from all former years or fall *above* the bound. The zero counts for Craig are the lowest in relation to earlier counts. Even these values fall within rounding of the 95 percent bound on the mean for Craig. Furthermore, these zero counts mirror zero counts in the earliest CBC records for this bay.

Counts in the past few years, then, corroborate the pattern observed in the years we analyzed most thoroughly. Christmas Bird Counts continue to provide little evidence for a broad, sustained decline in marbled murrelets in Southeast Alaska.

Acknowledgements

Discussions with R. King, Biometrician, Rocky Mountain Forest and Range Experiment Station, and E. O. Garton, University of Idaho, provided insight into the analysis of trend data. J. Bart, C. Martinez del Rio, M. Raphael, and several anonymous souls reviewed early copies of the manuscript; we thank each of you. The U.S. Forest Service Rocky Mountain Forest and Range Experiment Station and the Pacific Northwest Research Station, U.S. Forest Service, Alaska Region, and University of Wyoming provided funding and support.

Literature Cited

Agler, B. A., S. J. Kendall, and D. B. Irons. 1998. Abundance and distribution of marbled and Kittlitz's murrelets in Southcentral and Southeast Alaska. Condor 100:254-265.

Belsey, D. A., E. Kuh, R. E. Welsch. 1980. Regression diagnostics: Identifying influential data and sources of collinearity. New York, NY. Wiley 292 p.

Bock, C. E. and T. L. Root. 1981. The Christmas Bird Count and avian ecology. Pages 17-23. in C. J. Ralph and J. M. Scott, eds. Estimating numbers of terrestrial birds. Stud. Avian Biol. 6.

Burger, A. E. 1995. Marine distribution, abundance, and habitats of marbled murrelets in British Columbia. Pages 295-312. *In*: C. J. Ralph, G. L. Hunt, M. G. Raphael, and J. F. Piatt. eds. Ecology and conservation of the Marbled Murrelet. Gen. Tech. Rep. PSW-GTR-152. Pacific Southwest Research Station, USDA Forest Service. 420 p.

Butcher, G. S. 1990. Audubon Christmas Bird Counts. Pages 5-13. in J. R. Sauer, and S. Droege. eds. Survey designs and statistical methods for the estimation of avian population trends. U.S. Fish Wildl. Serv., Biol. Rep. 90. 166 p.

Carter, H. R. and S. G. Sealy. 1990. Daily foraging behavior of marbled murrelets. Studies in Avian Biology 14:93-102.

Carter, H. R. and K. J. Kuletz. 1995. Mortality of marbled murrelets due to oil pollution in North America. Pages 261-270. *In*: C. J. Ralph, G. L. Hunt, M. G. Raphael, and J. F. Piatt. eds. Ecology and conservation of the Marbled Murrelet. Gen. Tech. Rep. PSW-GTR-152. Pacific Southwest Research Station, USDA Forest Service. 420 p.

Carter, H. R., M. L. McAllister and M. E. Isleib. 1995. Mortality of marbled murrelets in gill nets in North America. Pages 271-284. *In*: C. J. Ralph, G. L. Hunt, M. G. Raphael, and J. F. Piatt. eds. Ecology and conservation of the Marbled Murrelet. Gen. Tech. Rep. PSW-GTR-152. Pacific Southwest Research Station, USDA Forest Service. 420 p.

Conover, W. J. and R. L. Iman. 1981. Rank transformations as a bridge between parametric and nonparametric statistics. Amer. Stat. 35:124-129.

Day, R. H., S. M. Murphy, J. A. Wiens, G. D. Hayward, E. J. Harner, and L. N. Smith. 1997. Effects of the *Exxon Valdez* oil spill on habitat use by birds in Prince William Sound, Alaska. Ecological Applications 7:593-613.

Daniel, W. W. 1978. Applied nonparametric statistics. Houghton Mifflin Company, Boston, Mass. 503 p.

Evans, M. I., P. Symens, and C. W. T. Pilcher. 1993. Short-term damage to coastal bird populations in Saudi Arabia and Kuwait following the 1991 Gulf War marine pollution. Mar. Pollut. Bull. 27:157-161.

Received 30 December 1997
Accepted for publication 30 June 1998

Harris, M. P. and S. Wanless. 1984. The effect of the wreck of seabirds in February 1983 on auk populations on the Isle of May (Fife). Bird Study 31:103-110.

Kendall, M. G. 1973. Time-Series. Hafner Press, New York, NY. 197 p.

Klosiewski, S. P. and K. K. Laing. 1994. Marine bird populations of Prince William Sound, Alaska, before and after the *Exxon Valdez* oil spill. Unpubl. report. *Exxon Valdez* Oil Spill State and Federal natural Resources Damage Assessment Final Report, prepared for *Exxon Valdez* Oil Spill Trustees Council, Anchorage, AK. (Available from the Oil Spill Public Information Office, 645 G St., Anchorage, AK 99501-3451.)

Murphy, S. M., R. H. Day, J. A. Wiens, and K. R. Parker. 1997. Effects of the *Exxon Valdez* oil spill on birds: Comparisons of pre- and post-spill surveys in Prince William Sound, Alaska. Condor 99:299-313.

Perry, D. A. 1995. Status of forest habitat of the marbled murrelet. Pages 381-383. *In*: C. J. Ralph, G. L. Hunt, M. G. Raphael, and J. F. Piatt. eds. Ecology and conservation of the Marbled Murrelet. Gen. Tech. Rep. PSW-GTR-152. Pacific Southwest Research Station, USDA Forest Service. 420 p.

Piatt, J. F. and P. J. Anderson. In Press. Response of murres (*Uria spp.*) to the *Exxon Valdez* oil spill and changes in the Gulf of Alaska marine ecosystem. In: J. Rice, B. Wright. eds. Proceedings of the *Exxon Valdez* oil spill symposium. American Fisheries Society.

Piatt, J. F., C. J. Lensink, W. Butler, M. Kendziorek, and D. R. Nysewander. 1990. Immediate impact of the *Exxon Valdez* oil spill on marine birds. Auk 107:387-397.

Piatt, J. F. and N. L. Naslund. 1995. Abundance, distribution, and population status of Marbled Murrelets in Alaska. Pages 285-294. *In*: C. J. Ralph, G. L. Hunt, M. G. Raphael, and J. F. Piatt. eds. Ecology and conservation of the Marbled Murrelet. Gen. Tech. Rep. PSW-GTR-152. Pacific Southwest Research Station, USDA Forest Service. 420 p.

Ralph, C. J., G. L. Hunt, M. G. Raphael, and J. F. Piatt. 1995. Ecology and conservation of the Marbled Murrelet in North America: an overview. Pages 3-22. *In*: C. J. Ralph, G. L. Hunt, M. G. Raphael, and J. F. Piatt. eds. Ecology and conservation of the Marbled Murrelet. Gen. Tech. Rep. PSW-GTR-152. Pacific Southwest Research Station, USDA Forest Service. 420 p.

Schempf, P. Research Scientist. U.S. Fish and Wildlife Service, Juneau, AK. [Personal communication]. June 1995.

USDA Forest Service, Alaska Region, 1991. Tongass National Forest land management plan revision. Supplement to the draft environmental impact statement. R10-MB-149. Anchorage, AK, 755 p.

U.S. Fish and Wildlife Service. 1992. Final rule listing the Marbled Murrelet as threatened in Washington, Oregon, and California. United States Federal Register, October 1, 1992.

Wiens, J. A. R. H. Day, S. M. Murphy, T. O. Crist, and G. D. Hayward. 1996. Effects of the Exxon Valdez oil spill on marine bird communities in Prince William Sound, Alaska. Ecological Applications 6:828-841.

H. Elizabeth Kirkpatrick, Department of Biology, University of Puget Sound, 1500 N. Warner, Tacoma, Washington, USA, 98416

Factors Affecting the Success of California Poppy (*Eschscholzia californica*) Introduced into Western Washington State

Abstract

California poppies (*Eschscholzia californica*), native to Californian grasslands, have been introduced to the south Puget Sound region and apparently persist along roadbanks and as volunteers in gardens, where the biomass of other vegetation is relatively low. Whether poppies can successfully invade other areas from these source populations may depend on the ability of poppies to withstand the abiotic environment and/or to compete with the established vegetation. To examine the potential for competition to limit California poppy success, I tested the effects of competition with perennial ryegrass (*Lolium perenne*), soil type, and wintering regime in a factorial experiment. Single poppy plants were grown outside in pots with from 0 to 32 ryegrass plants, either previously established or simultaneously seeded, in relatively dry or moist soil. Half these pots were harvested in the fall; the rest were overwintered outside or inside the greenhouse.

Competition with established ryegrass prevented successful establishment of almost all poppy plants. Competition with simultaneously-seeded ryegrass caused mortality of poppy plants only at the highest densities; however, vegetative biomass, fruit number, and seed mass all decreased with increasing ryegrass biomass. Poppies were bigger and produced more fruits and seeds in moist soil, but soil type did not alter the intensity of competition. Poppy winter survival outside depended heavily on ryegrass abundance; competition with ryegrass significantly decreased survival of the plants wintered outside. These results suggest that competition from existing vegetation may relegate California poppies to sites where vegetation is sparse because of drought, low nutrients, or disturbance.

Introduction

How important is interspecific competition in determining which species are present in a community? This question has been of central interest to ecologists for several decades. Much debate has focused on the role of interspecific competition in ecological processes such as assembling communities (Diamond 1975; Connor and Simberloff 1979, 1983; Diamond and Gilpin 1982; Simberloff and Connor 1982; Moulton and Pimm 1983), controlling species' abundances (Tilman 1982, numerous reviews in Diamond and Case 1986), and allowing or preventing invasions by non-native species (Bazzaz 1986, Moulton and Pimm 1986, Newsome and Noble 1986, Pimm 1989, 1991).

Though not native to the Puget Sound region, California poppy (*Eschscholzia californica* Cham. (Papaveraceae)) has been introduced to the region by local gardeners and in wildflower mixes seeded along highways, and it persists sporadically in gardens and roadsides. California poppy has a rather high invasive potential, as demonstrated by its successful invasions of other regions with Mediterranean climates such as central Chile (Frias et al. 1975). However, it presently persists only sporadically in the Puget Sound region. Given its invasive potential, why has California poppy remained relatively sparse after its introduction to western Washington?

An introduced species may be limited in its spread either by physical and chemical conditions or by biological interactions (Pimm, 1991; Begon et al. 1996). The south Puget Sound region differs in both climatic conditions and species composition from the California grasslands to which California poppy is native. California poppies survive and reproduce in the Puget Sound region. However, they do so sporadically, indicating that one or more conditions limit their success in the region. This paper reports the results of a pot experiment designed to test the potential for interspecific competition to limit California poppy abundance.

One of the major differences in vegetation between the habitats occupied by California poppy in the south Puget Sound region and those of its native California grasslands is that the post-deforestation vegetation in south Puget Sound is dominated by perennial grasses rather than the annual grasses that now dominate the Californian grasslands. Competition with perennials may be more severe than with annuals because established perennials generally initiate growth earlier,

© 1998 by the Northwest Scientific Association. All rights reserved.

accumulate aboveground biomass more rapidly upon initiation of growth (Tilman 1988), and more quickly sequester limiting soil resources with their established root systems.

I investigated whether the success of California poppies is influenced by the biomass of surrounding vegetation, whether soil moisture influences their success, and whether poppies can survive the colder winter environment in the south Puget Sound region. I was interested in answering four specific questions regarding the success of California poppy in south Puget Sound: 1) Does neighboring vegetation decrease California poppy fitness (survival, vegetative biomass, fruit number, and seed biomass), and if so, how intense is that competition? 2) Does competition differ between seedling neighbors (more similar to annuals) and established neighbors (perennials)? 3) Is the intensity of competition from neighbors more severe in moist soil than in drier soil? and 4) Are poppies able to survive winter temperatures in the south Puget Sound region and is that survival influenced by competition?

Materials and Methods

Species Description

California poppy is a short-lived perennial or facultative annual native to grasslands of California and Oregon. It is generally outcrossed (Cook 1961), with bumblebees as the main pollinators. The showy flowers develop into elongated capsules that burst at maturity, ejecting seeds approximately 1 m (Robinson et al. 1995). The recognized native range of California poppy is described as California north to the Columbia river (Hitchcock and Cronquist 1973). In the central valley of California, California poppies are one of the few native species that still occur abundantly within the introduced annual grasslands (Robbins et al. 1951, Munz and Keck 1959, Cook, 1965). These introduced grasses are Mediterranean in origin and have been very successful in California's Mediterranean climate. Prior to the invasion by these annual grasses, the California grasslands were occupied by perennial grass species. Presently, most species of the California grasslands, including California poppy, germinate in the cool, wet winter and flower and set seed during the spring and summer (Robinson et al. 1995). In contrast, poppies in the south Puget Sound region germinate in the spring (March-April) or fall (October-November). Spring-germinated seedlings can reproduce their first year, generally blooming from August until frost. Perenniating plants bloom much earlier, from late March until frost, and mature seed is produced starting in late June.

Poppies in the south Puget Sound region usually occupy treeless habitats with a wide variety of soil types. Naturally-occurring seedlings are found most often where other herbaceous cover is sparse (personal observation). Such sites are commonly steep, south- or west-facing hillsides with relatively poor, dry soils or disturbed areas such as graveled roadsides that may have richer soils. Individual poppy plants are typically surrounded by a mixture of introduced, largely annual, grasses (e.g., *Bromus mollis, B. rigidus, B. tectorum, Festuca myuros*), but including some perennial grasses (e.g., *Dactylis glomerata, Lolium perenne, Holcus lanatus, Agrostis alba*), and several introduced forbs (e.g., *Cytisus scoparius, Hypericum perforatum, Rumex acetosella, Sonchus oleraceus, S. asper*). In some of the dry soil habitats, poppy populations are apparently persistent (personal observation), but have not spread beyond a small area.

Experimental Design

To compare the effects of competition between established and seedling perennial grasses, between moist and dry soil, and on winter survival, I set up a three-way factorial additive experiment. An additive experiment is more appropriate than a substitutive experiment to the question of poppy establishment in surrounding vegetation and for measuring the intensity of competition (Goldberg and Scheiner 1993). To quantify the intensity of competition, I grew individual poppy plants with perennial ryegrass (*Lolium perenne*). Single poppy targets were grown with ryegrass at one of seven densities (0 , 1, 2, 4, 8, 16, or 32 grass plants per 12.5 cm diameter pot). I grew poppies with ryegrass planted at two different times to compare the effects on poppies of simultaneously-sown ryegrass with those of established ryegrass. In half of the pots of each density treatment, ryegrass seeds were planted two months before poppy seeds to allow ryegrass to establish; in the high neighbor density treatments, ryegrass covered roughly 75% of the surface area of the pot when the poppy seeds were planted. In the other half of the pots, ryegrass seeds were planted simultaneously with poppy seeds. To examine the effects of variation in soil type, two different soil mixes [100% Sunshine® potting mix (moist soil) and 50% potting mix and

50% Perlite® (dry soil)] were compared. These different soil types induced documented differences in water availability (see below) and presumed differences in nutrient availability. Thus, a treatment combination is defined by one of seven ryegrass densities, one of two ryegrass planting times, and one of two soil types. Finally, to test winter survival of poppies, I overwintered half the surviving poppies in each treatment combination outside and the other half inside a greenhouse.

Each treatment combination was replicated 8 times for a total of 224 pots. These pots were placed on greenhouse benches outside on a roof terrace at the University of Puget Sound campus in Tacoma, WA, USA (47°15' N, 122°30' W), during the summer of 1994. For all pots, I used commercially available seeds of California poppy and perennial ryegrass. Although I would have preferred using seeds produced by the locally adapted poppy populations, they were unavailable until much later than the necessary initiation date.

Poppies were planted 26 May 1994 and thinned to one poppy target individual per pot after germination. All pots were kept watered to field capacity during seedling establishment. Seedlings became established in all pots, and then I watered (to field capacity) only when natural rainfall was insufficient to keep grasses from showing signs of water stress.

In mid-July, I weighed each pot before and after watering to assess differences in total water held between the two soil types: the pots with the Perlite/potting soil mix held significantly less water than the pots with 100% potting soil (means of 70 pots per group were 506.0 and 666.1 g water per pot, respectively; $t = 10.94$, $P < 0.0001$).

I collected mature fruits from each poppy target daily, cutting the stem just below the swollen receptacle to collect all tissue dedicated to reproductive activity. On 12 September, 1994, I collected remaining fruits from all plants and recorded the survival of all poppy target individuals. Then, from each treatment combination, I randomly selected for harvest half the pots with a living poppy. Harvesting a pot consisted of cutting the ryegrass plants at soil level and extracting the poppy target from the soil by washing the soil away from the orange roots of the poppy target. The ryegrass shoots, the poppy shoot, and the poppy root from each pot were wrapped in separate newspaper envelopes, labeled, and dried for 5 days at 50° C. I weighed each dried poppy component as one measure of performance and weighed the ryegrass shoots as a more precise measure of neighbor abundance than density class. Ryegrass roots were too difficult to extract from the soil to be harvested. I also dried and weighed reproductive components (receptacles, fruits, and seeds). Because all of these reproductive biomass measures gave qualitatively similar results, data are presented only for seed biomass.

The pots I did not harvest were randomly assigned within treatment combination to winter inside the greenhouse or outside on the terrace. Pots inside the greenhouse were watered to capacity when necessary to prevent signs of wilting in the ryegrass. Outside pots were watered with natural rainfall. The following spring (May 1995), I recorded the survival status of all overwintered poppy target individuals.

Data Analysis

Survival data, both for the growing season and for the winter, were analyzed using Chi-square goodness of fit tests for the main effects and Chi-square tests of independence for interactions between treatment factors. Poppy vegetative biomass, number of fruits, and seed biomass were analyzed both on an absolute and on a relative basis. To convert absolute biomass to relative biomass, each biomass within a timing x soil type treatment combination was divided by the mean biomass for poppy targets with no ryegrass neighbors in that treatment combination. These measures were analyzed using ANCOVAs, with ryegrass biomass as a covariate. All statistical analyses were carried out using SYSTAT 5.2 statistical software (Wilkinson et al., 1992).

Results

Poppy Survival

Almost no poppy target individuals survived in the established ryegrass whereas many survived in the simultaneously-seeded ryegrass (Table 1, planting time main effect). Of the 96 poppy individuals that germinated in pots with established ryegrass, only 2 survived the summer, and these were in pots with only a single ryegrass plant in the drier soil (Figure 1a). In contrast, where no ryegrass neighbors were present, all eight poppy target individuals survived in each soil type. Ryegrass density decreased the survival of poppies (Table 1, ryegrass density main effect; Figure 1), with established

TABLE 1. Chi-square test results for poppy summer survival. Each treatment combination began with eight replicates. Main effect tests of planting time and ryegrass density used all cells; the planting time x density interaction pooled the three lowest density classes to minimize cells with expected numbers less than five.

Comparison	df	X^2	P
Planting time	1	42.7	< 0.0001
Ryegrass density	6	44.5	< 0.0001
Planting time x density	4	33.3	< 0.0001

ryegrass neighbors having a much greater negative effect on survival than simultaneously-seeded ryegrass neighbors (pooling the last three ryegrass densities to minimize cells with expected numbers less than five; Table 1, timing x density interaction). In simultaneously-seeded ryegrass, all poppy target individuals survived except in the two highest density ryegrass treatments (16 and 32 neighbors; Figure 1b). With 16 ryegrass neighbors, 25% of poppy targets survived; with 32 ryegrass neighbors, no poppy target individuals survived. Soil type had no significant effect on survival in either established ryegrass or in simultaneously-seeded ryegrass (df = 1, P = 0.593 and P = 0.913, respectively).

Poppy Vegetative Biomass

Because so few poppies survived in the established ryegrass treatment, I analyzed poppy vegetative biomass only for the simultaneously-seeded ryegrass treatment. The results of analyses on absolute and relative bases were similar for two effects: ryegrass biomass reduced total poppy vegetative biomass markedly (Table 2, ryegrass biomass main effect; Figure 2a), and the negative effect of ryegrass was similar between the two soil types (Table 2: absolute

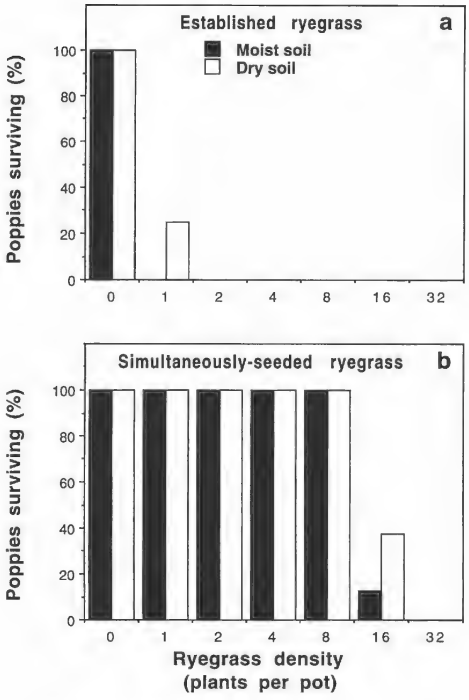


Figure 1. Poppy survival during summer in (a) established ryegrass and (b) simultaneously-seeded ryegrass. Each treatment combination started with eight replicates. Survival was much worse in established ryegrass than in simultaneously-seeded ryegrass (P < 0.0001) and with higher ryegrass densities (P < 0.0001). Density had a more severe effect in established ryegrass than in simultaneously-seeded ryegrass (using only the lowest three density categories, P = 0.0002).

TABLE 2. ANCOVA results (P-values, sample sizes, and R^2) from analysis of poppy fitness measures. Relative measures were adjusted by dividing each value by the mean biomass in the zero neighbor control (each soil type calculated separately).

Absolute measures	Ryegrass biomass	Soil type	Ryegrass x soil interaction	N	R^2
Vegetative biomass	<0.0001	0.003	0.724	39	0.824
Fruit number	<0.0001	0.013	0.694	20	0.719
Seed biomass	<0.0001	<0.0001	0.127	21	0.814
Relative measures					
Vegetative biomass	<0.0001	0.386	0.240	39	0.802
Fruit number	0.0002	0.407	0.202	20	0.655
Seed biomass	<0.0001	0.670	0.662	21	0.767

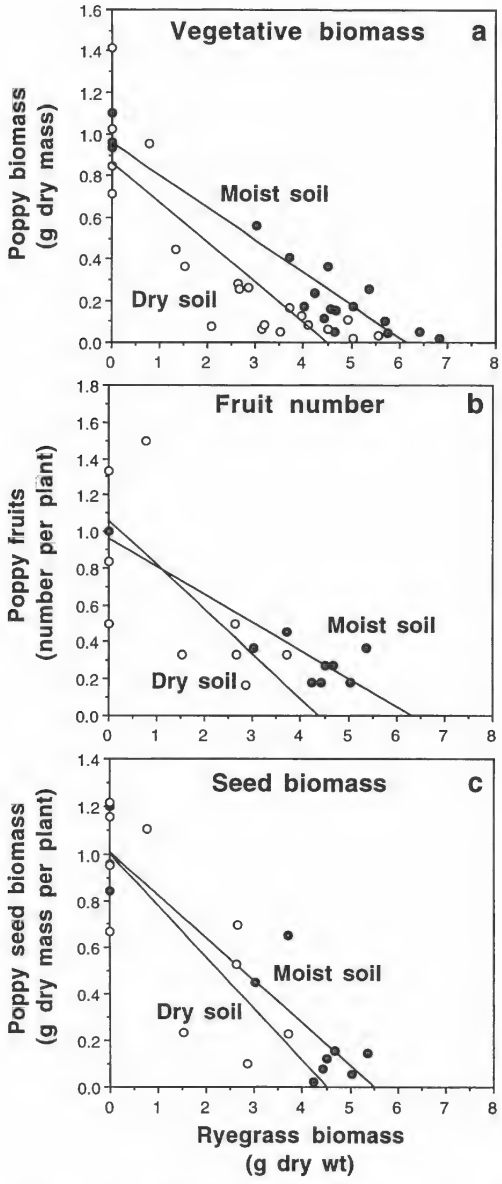


Figure 2. Effects of ryegrass competitors on (a) vegetative biomass, (b) fruit number, and (c) seed biomass of California poppy in moist and dry soils. All poppy measures are presented on a relative basis wherein each poppy biomass with ryegrass neighbors was divided by mean poppy biomass when no ryegrass neighbors were present. Only data from the simultaneously-seeded treatment were analyzed. Increasing ryegrass biomass decreased all measures of poppy performance, and in no case did the intensity of that competition differ between moist and dry soils. When measured on an absolute basis, all measures of poppy performance were higher on moist soils than on dry soils. (a) Increasing ryegrass biomass decreased poppy biomass ($P < 0.0001$; moist soil: $Y = 0.959 - 0.156X$, $R^2 = 0.908$; dry soil: $Y = 0.860 - 0.191X$, $R^2 = 0.735$). (b) Increasing ryegrass biomass decreased fruit number ($P = 0.0002$; moist soil: $Y = 0.810 - 0.128X$, $R^2 = 0.883$; dry soil: $Y = 0.987 - 0.226X$, $R^2 = 0.495$). (c) Increasing ryegrass biomass decreased seed biomass ($P < 0.0001$; moist soil: $Y = 1.066 - 0.193X$, $R^2 = 0.860$; dry soil: $Y = 1.00 - 0.221X$, $R^2 = 0.601$).

and relative soil x ryegrass interactions). However, on an absolute basis, poppy targets accumulated higher biomass in the moist soil than in the dry soil (Table 2, absolute soil type main effect), whereas on a relative basis, that difference was eliminated by the relativizing process (Table 2, relative soil type main effect). In an analysis of root/shoot ratio, one very small target individual in the dry soil was recognized as an outlier and removed [residual was tested after regression against ryegrass biomass using Grubb's test (Rohlf and Sokal 1981; statistic = 4.25, n = 21, $P < 0.005$)]. Root/shoot ratio increased as ryegrass biomass increased ($F_{1,34} = 4.96$, $P = 0.033$), but did not differ with soil type ($F_{1,34} = 0.023$, $P = 0.880$).

Poppy Fruit Number and Reproductive Biomass

Of the 102 poppy target individuals surviving, only 59 set fruit. One of these fruiting plants in the simultaneously-seeded ryegrass treatment had been infested with aphids and set 66% more fruits than any other plant. This individual was removed from the fruit number variable as an outlier by Grubb's test (statistic = 4.27, n = 59, $P < 0.005$). However, because this individual's many fruits were small, it was not an outlier and was included in the analyses of the reproductive biomass variables. Excluding this plant, 47 surviving poppy target individuals from the simultaneously-planted ryegrass treatment were harvested, and of these, 29 set fruit. Fruit number decreased significantly with increasing ryegrass biomass (Table 2, Figure 2b). Mean fruit number in moist soils (10.6 fruits/plant) was almost double that in dry soils (6.0 fruits/plant, Table 2, absolute soil type main effect). The decrease in fruit number with higher ryegrass biomass was similar between the two soil types, whether measured on an absolute or relative basis (Table 2, absolute and relative soil x ryegrass interactions).

Seed biomass of poppies in the simultaneously-seeded ryegrass treatment decreased with ryegrass biomass (Table 2, ryegrass biomass main effect; Figure 2c), and was higher in moist soils than in dry soils (Table 2, absolute soil type main effect). The effects of ryegrass biomass on seed biomass did not differ between soil types whether measured on an absolute or relative basis (Table 2: absolute and relative soil x ryegrass interactions). However, another measure of reproductive success, fruit biomass, did differ in its response to ryegrass biomass between soil types depending on whether they were measured on an absolute or relative basis. On an absolute basis, fruit biomass decreased more per gram of ryegrass in moist soil than in dry soil ($P = 0.046$, $r^2 = 0.874$). On a relative basis, however, fruit biomass did not differ in its response to ryegrass biomass between soil types.

Poppy Winter Survival

Whereas half the poppies with no ryegrass neighbors survived outside the greenhouse, no poppies in competition with ryegrass survived the winter outside (Figure 3a). Poppy plants wintered inside the greenhouse survived much better than those wintered outside the greenhouse (Table 3, wintering location main effect). Ryegrass density reduced poppy survival much more severely outside the greenhouse than inside (Table 3, location x density interaction): 19 of 24 poppy target individuals survived inside the greenhouse, with survival unrelated to soil type ($X^2_{1\,df} = 1.00$, $P = 0.371$) or ryegrass density ($X^2_{2\,df} = 1.37$, $P = 0.504$).

Discussion

The south Puget Sound region (Olympia and Tacoma area) is slightly warmer and drier than much of the rest of the Puget Trough Province (Franklin and Dyrness 1973). Other such pockets of warm and dry conditions occur on the northeast coast of the Olympic Peninsula and on southwest exposures in the San Juan Islands. Lyons and Merilees (1995) also indicate similarly warm and dry conditions may occur on southeastern Vancouver Island and the Gulf Islands in British Columbia. As such, these areas may be more favorable for California poppy to persist than other sites within the Puget Sound region. The pre-European northern range limit of poppies was just north of the Columbia River (Hitchcock and Cronquist 1973), suggesting that the cooler winter temperatures of the Puget Trough limited the northward expansion of poppies. After being artificially introduced to the warmer microclimate of the south Puget Sound region, poppies might now be persisting near the limits of their physiological tolerance. As such, small variations in environmental factors such as soil moisture or

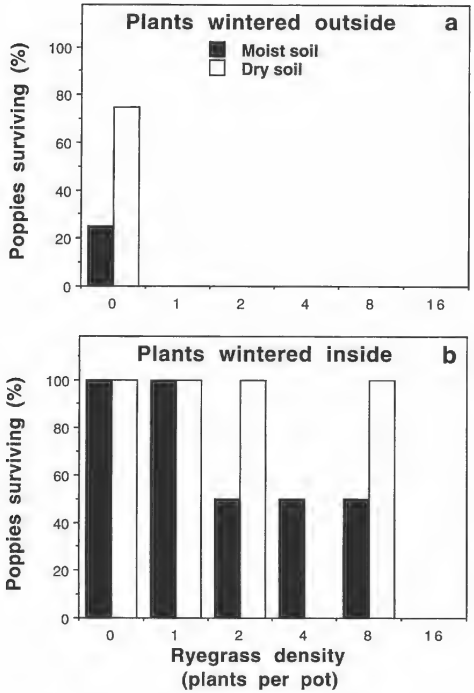


Figure 3. Poppy survival when wintered (a) outside and (b) inside the greenhouse. Sample sizes were four pots in each treatment combination (density x soil type). Ryegrass density had a much more severe negative effect on winter survival outside than inside (P = 0.0008) and poppies wintered inside survived much better than those wintered outside (P = 0.002). Winter survival inside was unrelated to soil type (P = 0.683) or ryegrass density (P = 0.129).

winter temperature may be critical, either alone or in conjunction with competition, to poppy establishment and survival. Results from the present experiment suggest that higher soil moisture increases poppy growth independently of competition, but that winter temperatures decrease poppy survival more drastically with competition than without. Moreover, competition has the potential to severely limit poppy success.

Established ryegrass precluded essentially all poppy survival whereas simultaneously-seeded ryegrass allowed poppy survival in all but the highest densities. This priority effect was so strong that even a single ryegrass plant established two months prior to poppy seeding excluded the poppy target in 14 of 16 pots. In contrast, densities of

TABLE 3. Chi-square test results for poppy winter survival. Cells were pooled over soil type and ryegrass densities (pots with two and four ryegrass neighbors were pooled and pots with eight and 16 ryegrass neighbors were pooled) so that each treatment combination began with 8 replicates. Wintering location and ryegrass density were tested as main effects and location x density was tested as an interaction.

Comparison	df	X^2	P
Wintering location	1	9.78	0.002
Ryegrass density	2	4.26	0.129
Location x density	2	9.78	0.0008

16 or more simultaneously-seeded ryegrass plants per pot were necessary to exclude any poppy target plants. These results are consistent with previous work on California poppies that showed that a simultaneously-seeded annual grass (*Avena fatua*) decreased poppy survival, growth and reproduction (Cook 1965). Cook compared poppy growth and reproduction with and without a single high density of *Avena* (seeded at approx. 2 plants/cm^2) in two large outdoor planter boxes. Unfortunately, because Cook used only a single *Avena* density, a comparison of the intensity of competition from the annual *Avena* with that from simultaneously-seeded perennial ryegrass is not possible.

Established perennials have previously been shown to have stronger competitive effects than annuals on the establishment of seedlings (Pearth and Foin 1985). When five species of grasses were sown into plots with either mixed annuals or a single dominant perennial, all five successfully established in the annual plots, and none established in the perennial plots. These authors attributed the difference in success to the quantity of above-ground biomass, and they confirmed this hypothesis by finding establishment success similar to that in the annual plots when the perennial plots were partially defoliated to match the biomass of the annual plots. Although the simultaneously-seeded perennials used in the present study are not annuals, their accumulation of biomass and pre-emption of resources in the first season is likely more similar to annuals than to established perennials. This interpretation leads to conclusions in the present study consistent with those of Perth and Foin, except for the increasing root:shoot ratio shown by the poppies as ryegrass biomass increased. However, in contrast to Perth

and Foin's result, higher allocation to roots under competition suggests that soil resources were more limiting than above-ground resources (Harper 1977, Chapin et al. 1987, Crick and Grime 1987, Tilman 1988, Wilson and Tilman 1995, but cf. Gedroc et al. 1996). This difference may result from growing the plants in pots rather than in the field, thus restricting their rooting volume. Alternatively, perhaps the perennial ryegrass seedlings allocated more assimilate to root tissue than an annual would have, thus increasing their capture of below-ground resources.

The effect of priority is likely to be based on both total biomass and biomass distribution. If a competing plant has roots infiltrating much of the available soil volume, then a new seedling will have a difficult time procuring soil resources. Similarly, existing shoot biomass positioned above the seedling will pre-empt light. Therefore, the establishment success of California poppy may well depend on the existing biomass at the potential establishment site. Robinson et al. (1995) tested the establishment and reproductive success of California poppies in the annual grasslands of California. They added poppy seeds to experimental plots that previously had no poppies present, and followed the success of these poppies as a function of species richness, disturbance, and dominance of a single species. They found that poppies were unable to establish in plots dominated by *Bromus diandrus*, an annual grass. They attributed this effect to the sequestration of limiting resources or the physical exclusion of poppies by the grass. Robinson et al. also found that small scale vegetation disturbance increased the germination success of poppies. Because they conducted a census every 10 days, their germination index included both actual germination and early seedling survival. Such early seedling survival might well have benefited from small scale animal disturbances that removed or trampled immediately adjacent biomass. However, because the focus of their study was on characteristics that affected invasibility of the plots, rather than on the causes of success or failure of poppy establishment, they did not manipulate or measure biomass of existing vegetation, and could not quantitatively assess the role of competition.

The intensity of the competitive effect of ryegrass can be compared between moist soil and dry soil on both an absolute and a relative basis. Comparing relative effects is probably a more accurate representation of long-term outcome (Goldberg and Scheiner 1993, Grace 1995). In the present experiment, on an absolute basis, poppies gained more biomass in moist soil across the entire ryegrass biomass range, but this effect was eliminated by the relativizing process (setting both intercepts to 1). Other than this soil moisture effect, vegetative biomass, fruit number, and seed biomass results did not differ between absolute and relative analyses. In contrast, fruit biomass did differ between absolute and relative analyses: on an absolute basis, fruit biomass was reduced more per gram of ryegrass biomass (i. e., greater competitive intensity) in moist soil than in dry soil, but on a relative basis, the competitive effect of ryegrass on poppy did not differ between soil types. This result is consistent with that of Campbell and Grime (1992), who found greater competitive intensity in higher resource conditions when measured on an absolute basis but equal competitive intensities when measured on a relative basis. Wilson and Tilman (1991, 1995) also found no difference in competitive intensity with increasing resource conditions when measured on a relative basis. This is not a consistent result among all studies, however. Kadmon (1995) found a higher competitive intensity in higher resource conditions using both absolute and relative measures. Kadmon suggested that inconsistency among studies sometimes may be explained by the range of competitor density or the range of resource levels used in studies. Kadmon's data (regression slopes in his Table 5) also apparently suggested that competitive intensity increased from low to moderate resource levels but then stayed constant or decreased from moderate to higher resource levels. This pattern holds whether using his absolute or relative competitive intensity measures.

Winter survival in pots may have underestimated survival rates in the ground, but the strong interaction between survival and competitive intensity is probably robust and has been observed previously (Woodward and Jones 1984). The dependence of winter survival on competitive intensity is likely to be mediated by carbohydrate storage. Larger stores of carbohydrate at the onset of winter, as evidenced by larger plants, have been positively correlated with winter survival in both foxglove (*Digitalis purpurea*) and ironweed (*Eupatorium cannabinum*, Woodward and Jones 1984). Because competition decreases plant size

and carbohydrate stores, it is also likely to decrease winter survival.

Populations of California poppies in temporarily disturbed habitats may encounter problems different from populations in sites where competing vegetation is chronically sparse. A single disturbance can temporarily reduce competing biomass, allowing poppy seedlings to establish a population. But as the surrounding vegetation regains biomass, it will compete more intensely with new seedlings. Even if those seedlings survive the summer, they may not have gained enough biomass to survive the winter. Because seedlings are typically much more susceptible to competition than adults (Harper 1977), poppy populations in which individuals must function as facultative annuals are more at risk of extinction than perennial populations. At sites where recurrent disturbance or low soil resources cause competing vegetation to remain sparse, populations may be fully capable of maintaining their presence. This interpretation suggests the hypothesis that populations of California poppies in the south Puget Sound region may be of two types: permanent populations—established and able to maintain themselves, or temporary—germinating, flowering, and reseeding only as long as the biomass of competing vegetation remains low. Greater disturbance introduced into the landscape by human expansion may allow poppies a higher frequency of temporarily favorable sites.

It is possible that cold hardiness or invasive ability may have been selected for in locally adapted populations. If so, winter survival or the ability of poppies to compete with established grasses may have been underestimated in this experiment because of the commercial origin of the seeds. Seeds produced by locally successful populations would have produced a more robust result, but were unavailable at the start of the experiment. Similarly, field tests of local soil and climatic factors, alone and in competition with naturally-occurring vegetation are imperative to assess the robustness of the results. Such field studies, using locally-collected seeds, are presently underway.

Acknowledgements

I thank D. Goldberg, S. Hannaford, S. Merritt, B. Rathcke, A. Tullis, P. Wimberger, and four anonymous reviewers for their insightful comments on previous versions of this manuscript, L. Clark for logistical assistance, and the University of Puget Sound Biology Department for financial support.

Literature Cited

Bazzaz, F. A. 1986. Life history of colonizing plants: some demographic, genetic and physiological factors. *In* H. A. Mooney and J. A. Drake (eds.) Ecology of Biological Invasions of North America and Hawaii, Springer-Verlag, New York. Pp. 96-110.

Begon, M., J. L. Harper, and C. R. Townsend. 1996. Ecology: Individuals, Populations and Communities, 3rd ed. Blackwell Science, Cambridge, MA.

Campbell, B. D. and J. P. Grime. 1992. An experimental test of plant strategy theory. Ecology 73:15-29.

Chapin III, F. S., A. J. Bloom, C. B. Field, and R. H. Waring. 1987. Plant responses to multiple environmental factors. BioScience 37: 49-57.

Connor, E. F., and D. Simberloff. 1979. The assembly of species communities: chance or competition? Ecology 60:1132-1140.

_____. 1983. Interspecific competition and species co-occurrence patterns on islands: null models and the evaluation of evidence. Oikos 41:455-465.

Cook, S. A. 1961. Genetic systems, variation, and adaptation in *Eschscholzia californica*. Evolution 16: 278-299.

_____. 1965. Population regulation of *Eschscholzia californica* by competition and edaphic conditions. Journal of Ecology 53:759-769.

Crick, J. C., and J. P. Grime. 1987. Morphological plasticity and mineral nutrient capture in two herbaceous species of contrasted ecology. The New Phytologist 107:403-414.

Diamond, J. M. 1975. Assembly of species communities. *In* M. L. Cody and J. M. Diamond (eds.) Ecology and Evolution of Communities, Harvard University Press, Cambridge, MA. Pp. 342-444.

Diamond, J. M., and T. J. Case (eds.). 1986. Community Ecology. Harper and Row, New York.

Diamond, J. M., and M. E. Gilpin. 1982. Examination of the "null" model of Connor and Simberloff for species co-occurrences on islands. Oecologia 52:64-74.

Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. U.S.D.A. Forest Service General Technical Report PNW-8.

Frias, D. L., R. Godoy, P. Iturra, S. Koref-Santibáñez, J. Navarro, N. Pacheco, and G. L. Stebbins. 1975. Polymorphism and geographic variation of flower color in Chilean populations of *Eschscholzia californica*. Plant Systematics and Evolution 123:185-198.

Gedroc, J. J., K. D. M. McConnaughay, and J. S. Coleman. 1996. Plasticity in root/shoot partitioning: optimal, ontogenetic, or both? Functional Ecology 10:44-50.

Goldberg, D. E., and S. M. Scheiner. 1993. ANOVA and ANCOVA: Field competition experiments. *In* S. M. Scheiner and J. Gurevitch (eds.) Design and Analysis of Ecological Experiments, Chapman and Hall, New York. Pp. 69-93.

Grace, J. B. 1995. On the measurement of plant competition intensity. Ecology 76:305-308.

Harper, J. L. 1977. Population Biology of Plants. Academic Press, New York.

Hitchcock, C. L., and A. Cronquist. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle.

Kadmon, R. 1995. Plant competition along soil moisture gradients: a field experiment with the desert annual *Stipa capensis*. Journal of Ecology 83:253-262.

Lyons, C. P., and B. Merilees. 1995. Trees, shrubs and flowers to know in Washington and British Columbia. Lone Pine Publishing, Redmond, WA.

Moulton, M. P., and S. L. Pimm. 1983. The introduced Hawaiian avifauna: biogeographic evidence for competition. American Naturalist 121:669-690.

_____. 1986. The extent of competition in shaping an introduced avifauna. *In* J. Diamond and T. J. Case (eds.) Community Ecology, Harper and Row, New York. Pp. 80-97.

Munz, P. A., and D. D. Keck. 1959. A California flora. University of California Press, Berkeley.

Newsome, A. E., and I. R. Noble. 1986. Ecological and physiological characters of invading species. *In* R. H. Groves and J. J. Burdon (eds.) Ecology of Biological Invasions: an Australian Perspective, Australian Academy of Science, Canberra. Pp. 1-20.

Pearth, D. R., and T. C. Foin. 1985. Analysis and prediction of population and community change: a grassland case study. *In* J. White (ed.) The Population Structure of Vegetation, Dr. W. Junk, Dordrecht, The Netherlands. Pp. 312-339.

Pimm, S. L. 1989. Theories of predicting success and impact of introduced species. *In* J. A. Drake, F. DiCastri, R. H. Groves, F. J. Kruger, H. A. Mooney, M. Rejmánek, and M. H. Williamson (eds.) Biological Invasions: A Global Perspective, Wiley, New York. Pp. 351-367.

_____. 1991. The Balance of Nature? University of Chicago Press, Chicago.

Robbins, W. W., M. K. Bellue, and W. S. Ball. 1951. Weeds of California. Sate of California Printing Division, Sacramento, CA, USA.

Robinson, G. R., J. F. Quinn, and M. L. Stanton. 1995. Invasibility of experimental habitat islands in a California winter annual grassland. Ecology 76:786-794

Rohlf, F. J., and R. R. Sokal. 1981. Statistical tables. W. H. Freeman and Co. New York.

Simberloff, D., and E. F. Connor. 1982. Missing species combinations. American Naturalist 118:215-239.

Tilman, D. 1982. Resource Competition and Community Structure. Princeton University Press, Princeton.

_____. 1988. Plant Strategies and the Dynamics and Structures of Plant Communities. Princeton University Press, Princeton.

Wilkinson, L., M. Hill, and E. Vang. 1992. SYSTAT: The system for statistics. Version 5.2. Systat, Inc., Evanston, IL, USA.

Wilson, S. D., and D. Tilman. 1991. Components of plant competition along an experimental gradient of nitrogen availability. Ecology 72:1050-1065.

_____. 1995. Competitive responses of eight old-field plant species in four environments. Ecology 76:1169-1180.

Woodward, F. I. and N. Jones. 1984. Growth studies of selected plant species with well-defined European distributions. I. Field observations and computer simulations on plant life-cycles at two altitudes. Journal of Ecology 72:1019-1030.

Received 15 September 1997
Accepted for publication 16 July 1998

Catherine G. Parks, USDA Forest Service, Pacific Northwest Research Station, La Grande, Oregon 97850

Larry Bednar, USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon 97208

and

Arthur R. Tiedemann, USDA Forest Service, Pacific Northwest Research Station, Wenatchee, Washington 98801

Browsing Ungulates—An Important Consideration in Dieback and Mortality of Pacific Yew (*Taxus brevifolia*) in a Northeastern Oregon Stand

Abstract

We examined 712 Pacific yew stems in a stand in the Blue Mountains to assess causes for yew dieback and mortality. Many living stems were dead or partially dead: 66% of the stems were <50% dead, 17% were >50% dead, and another 17% of the stems were dead. A high proportion (89%) of the mature stems had wounds. Assessment of wounding indicated that bark stripping by deer and elk was the primary cause and suggests that this factor is important in dieback and death of Pacific yew in the study area. Counts of seedlings and assessment of seedling age showed that most seedlings were between 1 and 3 years old with substantially fewer in the 3- to 6-year age class. Older seedlings were scarce. Severe damage to mature stems and lack of seedling recruitment (presumably because of ungulate browsing) raise questions about the continued viability of Pacific yew in this area.

Introduction

In the Blue Mountains of northeastern Oregon, Pacific yew (*Taxus brevifolia* Nutt.) grows as small trees associated with five grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.) forest community types: grand fir/*Gymnocarpium dryopteris* (L.) Newm.; grand fir/*Polystichum munitum* (Kaulf.) Presl var. *munitum--Asarum caudatum* Lindl.; grand fir/*Trautvetteria caroliniensis* (Walt.) Vail.; grand fir/Pacific yew/*Clintonia uniflora* Kunth; and grand fir/Pacific yew—*Linnaea borealis* L. var. *longifolia* Torr. (Johnson and Clausnitzer 1992). These forest communities are characteristically cool, moist environments with long fire intervals. Forest types with Pacific yew are highly productive and thus receive intensive forest management for timber.

Pacific yew occupies only a small percentage of the Blue Mountains landscape, but it is an important component of many forest habitats that coincide with the summer and fall range of mule deer (*Odocoileus hemionus hemionus*) and elk (*Cervus elaphus nelsoni*). Pacific yew foliage is a favorite browse of large ungulates (Bolsinger and Jaramillo 1990, Pierce and Peek 1984). In areas in the Blue Mountains where Pacific yew grows, the foliage was the most consistently eaten browse species throughout the summer and composed up to 23% of the elk diet during late summer (Korfage et al. 1980). Repeatedly browsed yews sometimes develop compact bushy crowns that grow close to the ground. Except for furnishing browse, the functions of yew in the ecosystem are largely unknown. The effects of protracted, extensive browsing on reproductive success, age structure, and mortality rates are poorly understood. Green and Ward (1991) report that current rates of moose (*Alces alces*) browsing in the Nez Perce National Forest in Idaho may prevent small yews from growing beyond browsing height. They suggested that a decline in the moose population may be required to allow yew sprouts and seedlings to develop into trees. Allison (1990, 1992) found that chronic browsing of Canada yew (*Taxus canadensis*) reduces fruit production and results in a higher proportion of male plants than in unbrowsed yew.

Evidence that ungulates alter the structure and composition of forest plant communities is widely reported (Bryant and Chapin 1986, Pastor et al. 1988, Tilghman 1989, Irwin et al. 1994, Schreiner et al. 1996). The ecological literature indicates that large-mammal herbivory can significantly influence forest ecosystem processes through effects on vegetation composition and productivity, successional rates, litter depth, and soil-nutrient concentrations (Irwin et al. 1994). Tilghman (1989) found that species composition of tree regeneration is significantly different between high and low deer-density treatments, and a shift to

© 1998 by the Northwest Scientific Association. All rights reserved.

near monocultures of a browse-tolerant tree species was predicted for the highest deer-density plots.

Our study was designed to survey and document the condition of Pacific yew in an unlogged fragment of forest with high mortality of Pacific yew. We collected data on yew mortality, dieback (death of the distal portion of a stem), the occurrence and likely cause of stem damage, vegetative layering, root sprouting, fruit production, and seedling age distribution. Our objective was to investigate the current status of yew in the stand by determining the causes of dieback and mortality and by evaluating vegetative and sexual reproductive status, seedling establishment, and seedling persistence. We used survey data to provide a framework for discussing how herbivory by large ungulates may significantly affect Pacific yew. For this study, the scope of inference was restricted to habitats supporting similar populations of Pacific yew and ungulates.

Study Area and Methods

The study was conducted in September 1992 on a 250-ha area (called West Sinks) 72 km north of La Grande, Oregon, in Union County. West Sinks ranges from 1158 to 1280 m in elevation and contains stands of old-growth grand fir with Pacific yew in the understory. Climate is a modified maritime system that moves from the Pacific Ocean through the Columbia River Gorge over landforms less than 300 m in elevation. Eighty to ninety percent of the 140 cm of precipitation measured at nearby High Ridge Evaluation Area falls between 1 October and 31 May (Fowler et al. 1987). Summer temperatures exceed 25 ^{0}C, and winter minima are typically between -5 and -10 ^{0}C. The area is underlain by surface flow volcanics, andesite, and old lacustrine deposits (Ehmer 1978). Soils are Typic Vitrandepts and Typic Cryandepts up to 125 cm deep that developed primarily from volcanic ash from Mount Mazama deposited about 6700 yr. B.P. (Ehmer 1978). West Sinks is an unlogged fragment but is completely surrounded by clearcut patches interspersed with successionally mature grand fir forests (Figure 1).

A high incidence of dieback and mortality of Pacific yew was found in the West Sinks area when the stands were examined for timber sale layout in September 1991 (report on file, Walla Walla Ranger District, Umatilla National Forest, Walla Walla, Washington). Although yews often had heavily browsed crowns, close examination showed that the dieback and mortality resulted from stem wounds caused by physical damage (Figure 2). Damage to stems appeared to be caused by bark stripping and removal of live cambium over many years. Wounds sometimes girdled the stem. Wounds were located on the stem from the ground up to a height not reachable by herbivores other than deer or elk. Wounded areas of the stem often had grooves that were of the size, spacing, and orientation of the incisors located on the lower jaw of elk. Elk hair occasionally was associated with wounds; hoof prints and fecal pellets were common throughout the area. No fungal decay or insect infestation appeared to be associated with wounds.

We systematically established belt transect lines 4.6 m wide and 310 m apart to sample 5% of the total area. For each Pacific yew stem taller than 0.5 m in the belts, we collected data on tree size, condition, presence or absence of wounded stems, cause of wound, and wound area (length by width). For wounds inconsistent with deer or elk bark-stripping, the cause was determined when possible. Animal-caused wounds, such as antler rubbing and bear clawing, as well as non-animal-caused mechanical wounding of known origin (tree falling) were recorded. Wounds with no obvious origin were recorded as "unknown cause."

To determine the stature of each stem, stem diameter, stem length, and total height were recorded. Condition of mature stems was assessed by evaluating the live crown under four classes: < 50% dead, > 50% dead (dying), 100% dead, recent (brown needles still attached), and 100% dead, old (no needles). We also documented whether the wound was made in the current year and thereby "fresh" (bright colored, moist) or clearly made in previous years (gray, dry) and thereby an "old wound".

In addition to individual stem data, reproductive information was systematically collected for every fifth yew tree or genet. Pacific yew propagate vegetatively similar to Canada yew as described by Allison (1990). Genets occur when individuals reproduce vegetatively by layering when their arching branches are pressed to the ground surface and take root. Side branches grow-

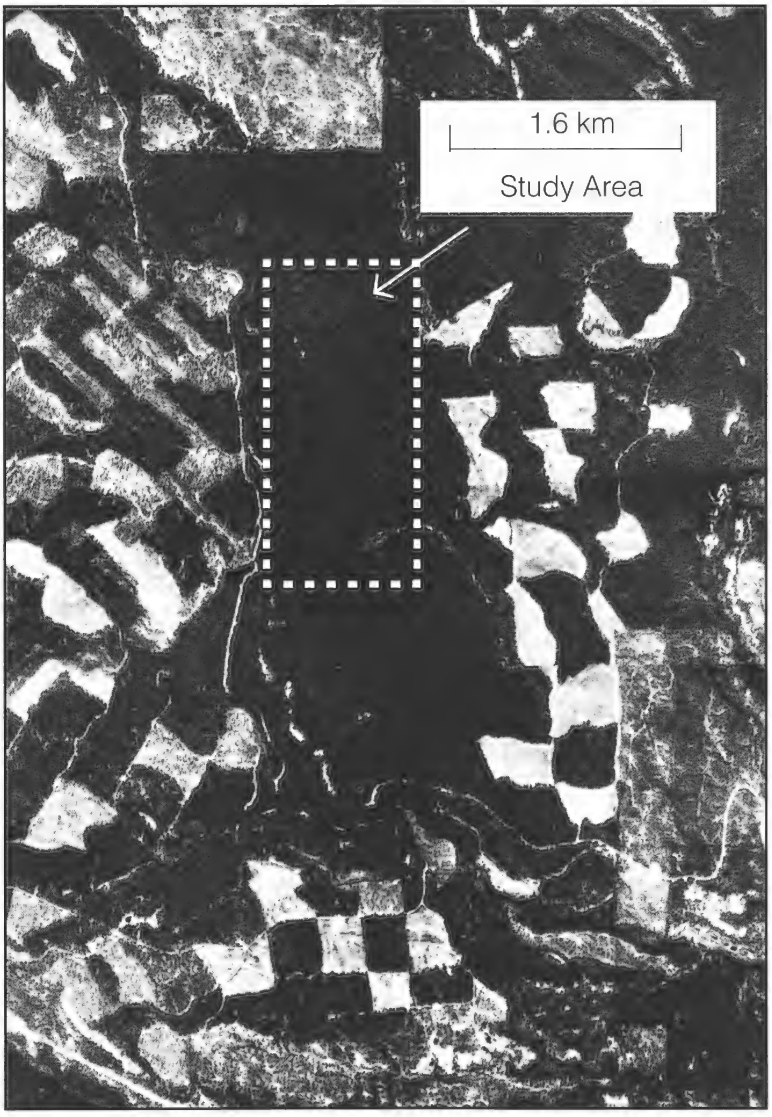


Figure 1. The West Sinks study area is located in undisturbed forest surrounded by an area of intensive timber management.

ing in different directions than that of the main stem axis cause the plant to spread along the forest floor. Connections between the rooted branches can be traced under the litter layer, but eventually these connections decay. In low-density populations such as in West Sinks, individual plants, or genets, consisting of one or more branches are readily distinguished. We defined a yew individual as a stem or shoot system emanating from the forest litter. Each individual consisted of one

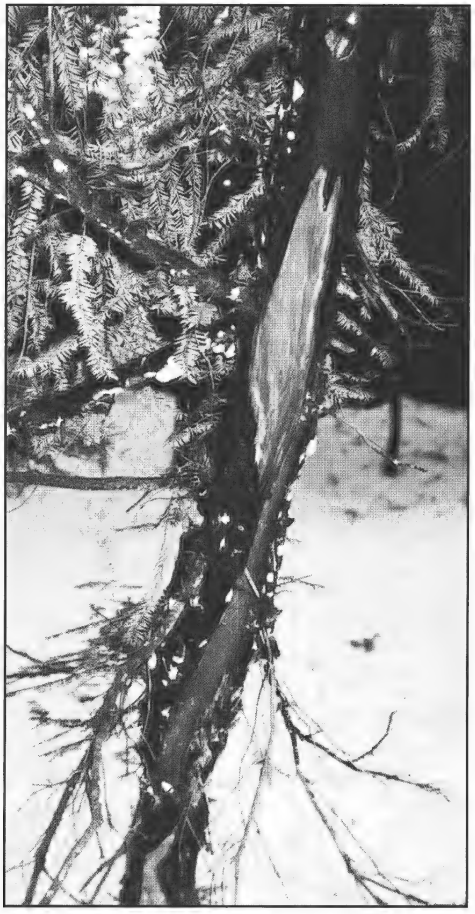


Figure 2. Stem wound on a Pacific yew caused by physical damage.

to four major stems that diverged from one another just above the litter. For every fifth yew tree we recorded presence of fruit, sprouts, and nearby seedlings. Sprouts grow from adventitious buds, roots, or the lower bole of already established plants. If they were large enough to bore, an increment core was extracted from the main stem base of fifth yew individuals or a neighboring stem at 0.25 m aboveground to determine age. Cores were collected from 37 trees. A 4-m radius, circular fixed plot was established that centered on the main stem of each fifth yew, and the plot was searched for seedlings. Seedlings were tallied, and their height and estimated age were recorded. Age was estimated by counting whorls of branchlets. A circular plot centering on the yew individual was chosen for seedling sampling because previous research shows that seedlings readily regenerate in the understory of parent trees and this method produces the highest probability of finding seedlings a stand. (Minore et al. 1996).

Pacific yew that were not seedlings but were under 0.5 m tall were tallied to determine the relative abundance of this size class. These plants were usually small stems that resulted from layering by a mature plant that had died. Pacific yew stems that were dead and down within the transect belts were measured to estimate their number. Dead stems with bark still attached were recorded as recent dead.

Fishers exact test (SAS Institute 1987) was applied to the data related to fruit and sprout production. Other quantitative comparisons were done through graphical and tabular displays.

Results and Discussion

From the 712 stems measured, 469 were rated as < 50% dead; 123 were 50-100% dead (dying); 86 were recent dead; and 34 were older dead. Stem damage or wounding was observed on 89% of the stems. We deduced that a high percentage of stem damage on yew in the West Sinks area is caused primarily by deer and elk, who use their teeth to incise, then strip and consume the bark (Figure 3). Nonfeeding damage by animals included antler rubbing, clawing by black bears, and hoof abrasions (Figure 3). Most of the wounds had occurred in prior years, and only a few wounds were recorded as fresh (7%) during the early September sample period. We speculate that the area may get heavier elk use later in the season because, during the previous year, many fresh wounds were observed by field crews in late September.

Although reports of animal herbivory on yew foliage are abundant, reports of bark stripping of yew are rare. An instance of bark stripping on Pacific yew by tame elk held in a temporary holding pen where no other tree species were debarked by the animals has been observed (John Cook, personal communication, National Council of the Paper Industry for Air and Stream Improvement, La Grande, Oregon). Likewise, Pierce (1984) reports evidence of bark stripping on yew trees by moose in northern Idaho where yew foliage is

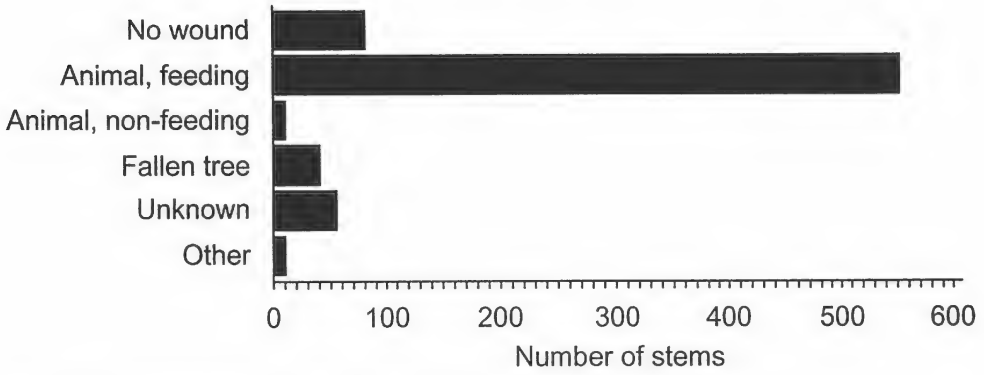


Figure 3. Incidence and subjective cause of wounds on Pacific yew stems.

considered critical to survival of resident moose (Crawford 1983).

Of the total number of yew stems that were dead and down (52), 22% were recent dead. Cores collected from stems ranging in diameter from 2.5 to 14.5 cm at 0.25 m aboveground had an age distribution of 83 to 87 years. The narrow range of establishment dates of the mature yew may suggest a light-intensity ground fire in the stand about 90 to 100 years ago. Minor fire scars were occasionally observed at the base of conifers distributed throughout the stand. Pacific yew is easily killed by light ground fire (McCune and Allen 1985), and previously existing yew may have been killed. The yew now present on the site may have regenerated from seed in a single cohort soon after a fire (Minore et al. 1996). In a separate study, cores taken throughout the West Sinks area determined the age of older overstory grand fir to be about 200 years and the larger, infrequent ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) and western larch (*Larix occidentalis* Nutt.) to be about 300 years old (Gene Paul, unpublished data, Pacific Northwest Research Station, Forestry and Range Sciences Laboratory, La Grande, Oregon). The age structure of Pacific yew compared to the age of the early seral species ponderosa pine suggests that yew is a late seral species in grand fir habitats (Busing et al. 1995, McCune and Allen 1985).

The incidence of small yew that were not seedlings but less than 0.5 m tall was infrequent; only 20 were found in the entire sample area. Yew reproduction (fruit, vegetative, seedlings) was low. Of the yew individuals examined for reproduction evidence, 5.5% had fruit present and 6% bore vegetative sprouts. From survey data, we detected a highly significant ($p < 0.001$) positive correlation between the presence of fruit and sprout production (Table 1). Because we did not determine the sex of each individual, we cannot state that a negative relation appeared between males and sprouting, although it may be implied by the data. The relevance of such a relation between sex and sprouting may be substantial in a yew management scenario that depends on resprouting stumps to maintain yew on a harvested site. Minore and Weatherly (1996) found that sprouting from stumps of harvested yew in western Oregon may be infrequent and should not be relied on to regenerate harvested stands. They did not determine the sex of harvested trees, but note that stump sprouts present before harvest tend to persist and be more vigorous than sprouts produced after harvest on stumps without preexisting sprouts. Our findings that sprouting may be related to sex is supported by a field observation (Charles Bolsinger, personal communication, Pacific Northwest Research Station, Forestry Sciences Laboratory, Portland, Oregon) in southern Oregon, where male yew tended to be single-stemmed and females often had numerous stems. An alternative hypothesis

TABLE 1. Association of fruit production with vegetative sprouting in Pacific yew.

	No Fruit	Fruit Present	Total
No Sprouts	218	6	224
Sprouts	7	6	13
Total	225	12	237

for our study would be that layering was not related to sex but was found on the most vigorous trees, that is, those trees with enough resources to produce both fruit and layers. In either case, because of the small sample size, these results should be interpreted cautiously.

Most seedlings were estimated to be 1 to 3 years old (Figure 4); older seedlings and saplings were conspicuously absent. We think that yew seedlings are consumed by ungulates once they are large enough to be recognized. Extirpation of seedlings by large ungulates is well documented, for example, Tilghman (1989) reports that, although many seedlings become established in all deer-density treatments, the number of seedlings that

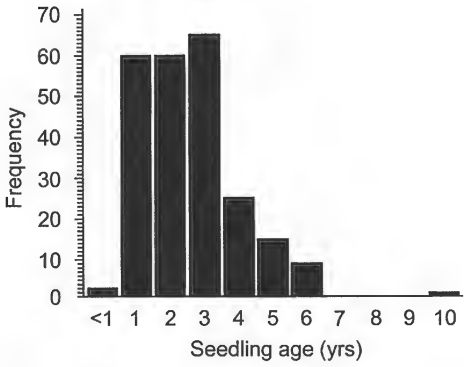


Figure 4. Age distribution of Pacific yew seedlings.

develop into the larger size classes is strongly affected by deer density.

We recognize that, in general, many factors in the forest environment other than large ungulate herbivory may influence seedling establishment and survival. Competition, poor growing conditions, herbivory from insects and small mammals such as mice and hares may influence seedling survival. Although some level of self-thinning occurs in most plant species during the course of establishment, shade-tolerant species such as yew generally survive and develop more height growth at a characteristic level of overstory competition than shade intolerant species if soil moisture and nutrients are not limiting (Oliver and Larson 1990). In contrast to the small number of yew seedlings observed at West Sinks, we found many yew seedlings of all ages in a nearby 26-year-old exclosure designed specifically to exclude deer and elk but not small mammals. The exclosure was constructed in a partially cut grand fir habitat in 1966 about 16 km from West Sinks and current conditions include dense overstory and understory vegetation (Riggs et al., in review). The presence of seedlings of various sizes in the exclosure and their absence in the similarly treated area surrounding the exclosure lend support to our speculation that deer and elk may be an important factor limiting the success of reproduction of yew from seed. Also, we saw no stem wounding of yew inside the exclosure.

Conclusions

Because of timber harvests, prescribed fire, and perceptions of Pacific yew as competitor of higher valued commercial conifer species, we believe that plant communities that support Pacific yew have been greatly reduced in the Blue Mountains over the last several decades. Our results indicate that Pacific yew also may be in a state of decline in unlogged, successionally mature grand fir habitats because of foraging on bark and seedlings by deer and elk. As an island of mature forest, West Sinks is likely preferred by big game in fall when nutrient concentration of understory vegetation is still relatively high (Vavra 1983), and optimal cover conditions provide for less snow accumulation and for security during hunting seasons (Witmer et al. 1985). Concentrations of ungulates may be the predominate factor in dieback and death of mature yew and of the recruitment potential of yew in West Sinks. The question then becomes, if yew is similarly affected throughout its range in the Blue Mountains province, can the species remain a viable entity in late successional grand fir stands? Past forest management practices combined with substantial growth in elk populations during the last several decades in the Blue Mountains (Irwin et al. 1994) could result in decline of yew and may extirpate some populations.

The prevalent practice of dispersing timber-harvest units and limiting their size was intended to optimize the arrangement of cover and open areas, not only for social concerns but also to maximize distributions of habitat for deer and elk, which often feed in openings and rest in adjacent stands of timber (Irwin et al. 1994, Thomas 1979). This strategy was widely implemented across the

landscape near the West Sinks area (Figure 1) and probably maximized herbivory, both in harvested units and adjacent forest stands, thereby facilitating damage to yew. As the single, large, continuous block of intact forest, West Sinks probably offers more attractive security cover to deer and elk, especially during hunting seasons, than do surrounding smaller blocks of forest.

Rational decisions for managing Pacific yew to maintain habitat diversity and sustainable productivity require an understanding of the present status of the plant. For management decisions at broad spatial scales, we need to know the extent of damage caused by browsing and other factors and to determine how these factors influence the ability of yew to survive throughout its range.

Literature Cited

Allison, T. D. 1990. The influence of deer browsing on the reproductive biology of Canada yew (*Taxus canadensis* Marsh.). Part I. Direct effect on pollen, ovule, and seed production. Oecologia 83: 523-529.

_____. 1992. The influence of deer browsing on the reproductive biology of Canada yew (*Taxus canadensis* Marsh.). Part III. Sex expression. Oecologia 89: 223-228.

Bolsinger, C. L., and A. E. Jaramillo. 1990. *Taxus brevifolia* Nutt. Pacific yew. *In* R. M. Burns and B. H. Honkala (tech. coords.), Silvics of North America: Volume 1, Conifers. Agric. Handbook 654. USDA, For. Serv., Washington, DC. Pp. 573-569.

Bryant, J. P., and F. S. Chapin. 1986. Browsing-woody plant interactions during plant succession. *In* K. Van Cleve, F. S. Chapin, P. W. Flanagan et al. (eds.), Forest ecosystems in the Alaskan taiga. Springer-Verlag, New York Pp. 213-225.

Busing, R. T., C. B. Halpern, and T. A. Spies. 1995. Ecology of Pacific yew (*Taxus brevifolia)* in western Oregon and Washington. Conservation Biology 9(5): 1199-1207.

Crawford, R. 1983. Pacific yew community ecology in north-central Idaho with implications to forest land management. University of Idaho, Moscow. Ph. D. Dissertation.

Ehmer, L. 1978. Soil resource inventory, Umatilla National Forest. USDA, For. Serv., Pac. Northw. Region, Portland, Oregon.

Fowler, W. B., J. D. Helvey, and E. N. Felix. 1987. Hydrologic and climatic changes in three small watersheds after timber harvest. USDA, For. Serv. Res. Pap. PNW-RP-379. Pac. Northw. Res. Sta., Portland, Oregon. 13 p.

Green, P., and R. Ward. 1991. Yew sprout assessment, Nez Perce National Forest, Idaho. Report on file with Pacific yew technical committee. USDA, For. Serv., Pac. Northw. Region, Portland, Oregon.

Acknowledgements

We thank Leonard Erickson and Mike Kemp (now retired) of the Oregon Department of Fish and Wildlife, and Edward Bottum, La Grande Oregon, for meaningful discussion. For study plan review and manuscript review, we thank Bob Riggs of Boise Cascade Corporation; John Cook, National Council of the Paper Industry for Air and Stream Improvement; Jack Walstad, Forest Resources Department, Oregon State University; Jerry Beatty, Bill Hopkins, and Fred Hall, USDA Forest Service, Pacific Northwest Region; Don Minore, (now retired) and John Kie, USDA Forest Service, Pacific Northwest Research Station; and two anonymous reviewers.

Irwin, L. L., J. G. Cook, R.A. Riggs, and J. M. Skovlin. 1994. Effects of long-term grazing by big game and livestock in the Blue Mountains forest ecosystems. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-325. Pac. Northw. Res. Sta., Portland, Oregon. 49. p.

Johnson, C. G., Jr., and R. R. Clausnitzer. 1992. Plant associations of the Blue and Ochoco Mountains. USDA, For. Serv., Pac. Northw. Region, R6-ERW-TP-036-92. Wallowa-Whitman National Forest, Baker City, Oregon. 164 p.

Korfage, R. C., J. R. Nelson, and J. M. Skovlin. 1980. Summer diets of Rocky Mountain elk in northeastern Oregon. J. Wildl. Manage. 44(3): 746-750.

McCune, B., and T. F. H. Allen. 1985. Forest dynamics in the Bitterroot Canyons, Montana. Can. J. Bot. 63: 377-383.

Minore, D., and H. G. Weatherly. 1996. Stump sprouting of Pacific yew. USDA, For. Serv. Gen. Tech. Rep. PNW-GTR-378. Pac. Northw. Res. Sta., Portland, Oregon. 6 p.

Minore, D., H. G. Weatherly, and M. Cartmill. 1996. Seeds, seedlings, and growth of Pacific yew (*Taxus brevifolia*). Northw. Sci. 70(3): 223-229.

Oliver, C. O., and B. C. Larson. 1990. Forest stand dynamics. McGraw-Hill, Inc. New York.

Pastor, J., R. J. Naiman, B. Dewey, and P. McInnes. 1988. Moose, microbes, and the boreal forest. BioScience. 38: 770-777.

Pierce, D. J. 1984. Shiras moose forage selection in relation to browse availability in north-central Idaho. Can. J. Zool. 62(12): 2404-2409.

Pierce, D. J., and J. M. Peek. 1984. Moose habitat use and selection patterns in north-central Idaho. J. Wildl. Manage. 48(4): 1335-1343.

Riggs, R. A., J. G. Cook, T. M. Tibbs, A. R. Tiedemann, P. Edgerton, M.Vavra, W. C. Krueger, F. C. Hall, L. D. Bryant, L. L. Irwin, and T. Delcurto. (In review) Successional trajectory of managed montane forests: influences of herbivory in the Blue Mountains ecological province. Manuscript on file with R. Riggs, Boise Cascade Corporation, La Grande, Oregon.

SAS Institute, Inc. 1987. SAS/STAT guide for personal computers, version 6. SAS Institute, Inc., Cary, North Carolina.

Schreiner, E. G., K. A. Krueger, P. J. Happe, and D. B. Houston. 1996. Understory patch dynamics and ungulate herbivory in old-growth forests of Olympic National Park, Washington. Can. J. For. Res. 26: 255-265.

Thomas, J.W., ed. 1979. Wildlife habitats in managed forests—the Blue Mountains of Oregon and Washington. USDA For. Serv. Agric. Handb. 533. Washington, DC. 512 p.

Tilghman, N. G. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. J. Wildl. Manage. 53(3): 524-532.

Received 7 July 1996
Accepted for publication 12 July 1998

Vavra, M. 1983. Managing grazing animal response to forestland vegetation. *In* B. F. Roche, Jr., and D. M. Baumgartner (eds.), Forestland grazing symposium. Washington State University, Pullman. Pp. 43-51

Witmer, G. W., M. Wisdom, E. P. Harshman, R. J. Anderson, C. Carey, M. P. Kuttel, I. D. Luman, J. A. Rochelle, R. W. Scharpf, and D. Smithey. 1985. Deer and elk. *In* R. E. Brown (tech. ed.), Management of wildlife and fish habitats in forests of western Oregon and Washington: Part 1—Chapter narratives. R6-F&WL-192. USDA For. Serv., Pac. Northw. Region, Portland, Oregon. Pp. 231-258.

J. Christopher Toney, Peter M. Rice, Division of Biological Sciences, University of Montana, Missoula, Montana 59812

and

Frank Forcella, North Central Soil Conservation Laboratory, U.S. Department of Agriculture, Agricultural Research Service, Morris, Minnesota 56267

Exotic Plant Records in the Northwest United States 1950-1996: an Ecological Assessment

Abstract

Nonnative plant species continue to be introduced into North America both accidentally and intentionally for horticultural and agricultural purposes. Some new species will spread extensively and some will become weeds of importance. We used a floristic database (INVADERS) to examine the status of incipient plant invasions in the northwest United States (Washington, Oregon, Idaho, Montana and Wyoming). We queried INVADERS for distribution records of plant species exotic to North America that were first recorded in the northwest states during 1950-1996. The query resulted in records for 288 species, of which 133 were judged to have become established (based on collector notes), or to have high potential to spread beyond artificial environments such as lawns and gardens. Inherent potential for invasion was based on examination of several invasive plant lists and the international literature on plant invasions. Thirty species have become moderately widespread (reported from >5 counties) in the five-state northwest region, and several are known to be aggressive invaders in other regions of North America or in other parts of the world. Five species discussed in the text are notable for rapid spread and/or indications of aggressiveness: *Polygonum cuspidatum* (syn: *Fallopia japonica, Reynoutria japonica*), *Bryonia alba*, *Impatiens glandulifera*, *Hieracium pratense* and *Scorzonera laciniata*. Compared with the early exotics (mid 1800s - early 1900s), which tended to be annual herbs, the post-1950 exotic flora shows a trend toward greater proportions of perennials and woody growth forms (shrubs and trees). Some applications of floristic databanks in regional-scale management of plant invasions are discussed.

Introduction

The establishment and spread of exotic plant species have occurred at high rates in North America since the time of European colonization (Forcella 1985, Mack 1986, 1989, Lesica et al. 1993, Rejmánek and Randall 1994), and constitute a major human effect on ecosystems (Usher 1988, Heywood 1989, Rice 1991, Beerling 1995, Vitousek et al. 1996). A large number of exotics, including many of today's most problematic weeds, became established in the northwest United States during the period 1850-1920 coincident with the influx of early agricultural settlers (Forcella and Harvey 1983). Important modes of introduction were contaminated crop seed, shipping ballast, adhesion to imported animals, and deliberate introductions of forage, ornamental and medicinal plants (Baker 1986, Mack 1986, 1991). The establishment of the western railroad network by 1890-1900 enhanced the potential for rapid and widespread dissemination of exotic plant propagules (Forcella and Harvey 1983; Mack 1989). Regional spread patterns have been primarily latitudinal (west-east) routes, corresponding to the interstate roadway and railway system, with important introduction centers occurring at junctions in the transportation network (Forcella and Harvey 1988). Despite improved quarantine measures and laws governing seed purity, new exotics have continued to arrive (Forcella 1985, Mack 1986, Westbrooks 1991). The rate of introduction is likely to remain high over the next few decades, due to both accidental introductions and intentional introductions for horticultural and agricultural purposes (Rejmánek and Randall 1994, Reichard and Hamilton 1997).

We examined the status of incipient plant invasions (1950-1996) using a large floristic database (Rice 1998). The database contained most of the potentially available distribution data on exotic plant species in the northwest United States. Our objective was to make a preliminary assessment of the recent exotic flora in relation to geographic extent of spread and reported invasive behavior within the region and elsewhere. Some potential applications of floristic databases in regional-scale management of plant invasions are also discussed.

© 1998 by the Northwest Scientific Association. All rights reserved.

Methods

We studied the five-state region in northwestern USA (the "northwest states") comprising Washington, Oregon, Idaho, Montana and Wyoming (latitude 41° - 49°N, longitude 104° - 124° 45' W). The five states cover a total area of 1,285,072 km^2. Boundaries of their 199 counties (avg. area 6,458 km^2) have been stable since the early 1900s (Cheney 1983, Yates and Yates 1987, Beck and Haase 1989).

INVADERS (Rice 1998) is a relational database containing ca. 80,000 distribution records for 3,022 plant species in Washington, Oregon, Idaho, Montana and Wyoming, spanning 1875-1996. Of these species, 868 are believed to be exotic to North America, and 75% of the distribution data are on the exotics. Fields include county, place name, date, collector and a comments field for miscellaneous low constancy data on associated vegetation, environmental factors, severity and size of weed infestations, etc. Sources are the following:

1. Herbarium records (38,576 total): Inventories of specimens (1875-1995) of exotic plant species and selected native species at Washington State University (WS, 10,877 records), Oregon State University (OSC, 10,011 records), Montana State University (MONT, 5,936 records), University of Montana (MONTU, 5,785 records), and University of Idaho (ID, 5,067 records); 703 records from University of Wyoming (RM); and smaller numbers of records from University of Washington (WTU), University of Oregon (ORE), Western Washington University (WWB), Willamette University (WILLU), Whitman College (WCW), University of British Columbia (UBC), and University of Idaho Collection of Forestry (IDF).

2. Extension Service identification records (17,421 total): 1990-96 for Washington, Oregon, Idaho and Montana, and records from 1949-90 compiled by Richard Old.

3. Agency records (16,477 total): U.S. Forest Service Region 1 ECODATA and Region 6 Ecology Plot data, the Oregon, Montana, Washington and Wyoming Departments of Agriculture, the Columbia River Basin Ecosystem Management Project 1995 weed survey data (Mike Karl, U.S. For. Serv.), and the Montana Weed Seed Free Forage Program.

4. Other records (7,550 total): Forcella and Harvey's (1988) original data, *Madroño*, data from Sheley (1994), and reports received and verified by Peter M. Rice (University of Montana).

Lack of a complete inventory of specimens at RM means that the exotic flora of Wyoming is currently under represented in the database, although the Forcella and Harvey (1988) data set does provide additional records based on specimens held at RM. Some new records could be added by a complete inventory at WTU, but records from WS (the largest herbarium in the region), OSC, and the Washington Extension Service provide good coverage of the state of Washington.

Nomenclature generally follows Hitchcock and Cronquist (1973). For species not in Hitchcock and Cronquist, Bailey et al. (1976), Tutin et al. (1964-80), Great Plains Flora Assoc. (1986), Hickman (1993), and Kartesz (1994) were consulted for accepted names and synonyms.

We queried INVADERS for exotic species first reported during 1950-1996. *Tamarix chinensis*, *T. ramosissima* (syn: *T. odessana*, *T. pentandra*), and *Tamarix* sp. all were first recorded in the northwest region ≥1955, but *T. gallica* was collected in Idaho as early as 1938 (Washington Co., *Christ 9409*, WS, ID; Owyhee Co., *Christ 9569*, ID). Because separation of these three species in the field is doubtful (Brock 1994), we treated them as a single taxon with earliest year of record 1938, thus excluding them from the present analysis. Also, *Chondrilla juncea* was excluded although it was not collected until 1965 in Kootenai County, Idaho (*Presby 24*, MONTU), but had been reported from near Spokane, Washington as early as 1938 (INVADERS record from Sheley 1994).

The initial species list was reduced by examining the individual distribution records. We assessed the ecological status of each species based on collector notes, if available, describing species abundance, associated vegetation, and site conditions. Each species was assigned to one of the following status categories: (1) Invasive—the distribution and/or abundance of the species in the wild is increasing regardless of habitat (Pyšek 1995), (2) Established—the species has been reported growing outside of cultivation in the northwest region, but the presence of self-regenerating populations undergoing further spread is uncertain, (3) Localized—the species has been reported as a waif or localized escapee in disturbed

environments, but longer range invasion within the region has not been reported, and (4) Unknown—no collector comments were available to assess the status of the species in the northwest region, meaning that some or all of the records for the species could be from horticultural settings. We omitted from the analysis species for which no comments had been recorded if we could find no other evidence of its invasion potential. Species were judged to have inherent potential for invasion if they had been reported in the literature as invasive in other temperate regions of the world or on the following invasive plant lists: Campbell (1997), Randall and Marinelli (1996), Parsons and Cuthbertson (1992), and the noxious weed lists for Washington, Oregon, Idaho, Montana, Wyoming and their neighboring states and provinces, California, Nevada, Utah, Colorado, Nebraska, South Dakota, North Dakota, Saskatchewan, Alberta and British Columbia. Universal access to the INVADERS database, including records for the excluded species, is provided via Internet at http://invader.dbs.umt.edu.

Results and Discussion

There were 1,349 distribution records for 288 species believed to be exotic to North America. The reduced list of species reported here (Appendix) consists of 133 species judged to have become established (based on collector notes), or to have high potential to spread beyond artificial environments such as lawns and gardens. Most of the post-1950 exotics have been reported from five or fewer counties, although several have become more widespread (6 to 25 counties, Figure 1). Only one species has been reported from >25 counties (*Polygonum cuspidatum*, 52 counties). Nineteen of the 133 species have been declared noxious in one or more northwest states. Fourteen species have been listed as noxious by Washington, seven by Oregon, four by Idaho, and one by Montana. Only one species is on the noxious weed list of more than two northwest states: *Crupina vulgaris* is noxious in Washington, Oregon, Idaho and Montana, and is also one of two species on the federal noxious weed list (Animal Plant Health Inspect. Serv. 1995). An additional six species not listed in any of the northwest states have been declared noxious in one or more neighboring states or provinces. Several other species have been reported as problematic in other regions of North America or on other continents.

Fig. 1

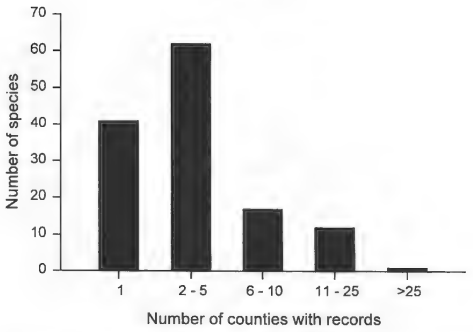


Figure 1. Histogram showing number of counties of record in Washington, Oregon, Idaho, Montana and Wyoming versus number of plant species exotic to North America and first recorded ≥1950 in the five-state region.

Some of the recent exotics in the northwest states have been spreading at rapid rates, and several species are in horticultural use but have been escaping frequently from cultivation.

Table 1 contains brief notes and references on 31 species of interest, selected subjectively based on review of the distribution records and plant invasion literature. Five species were chosen for additional discussion in the following section.

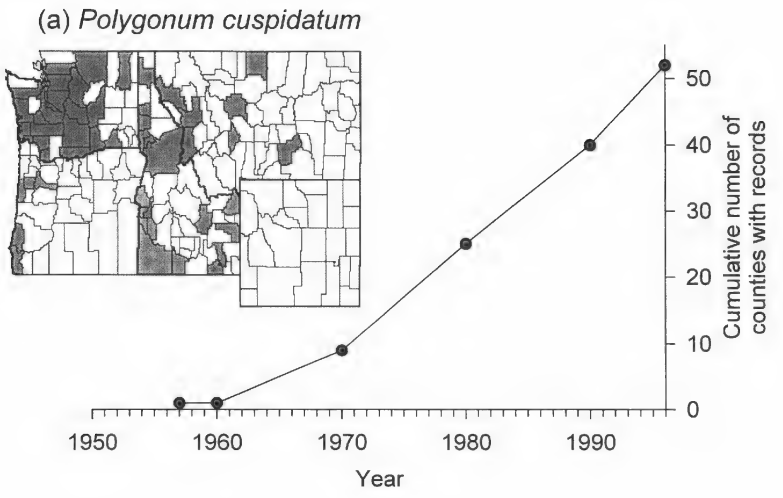
Species Notable for Rapid Spread and/or Indications of Aggressiveness

Japanese knotweed *Polygonum cuspidatum* (Polygonaceae; syn: *Fallopia japonica*, *Reynoutria japonica*) is native to southeast Asia (Japan, North and South Korea, Taiwan and China) and was introduced into Europe ca. 150 years ago (Beerling et al. 1995). It has become widespread, invading lowlands and some mountainous regions (to 900 m) from northern Portugal and Spain at 42° N latitude to the coasts of Norway and Finland at 63° N latitude (Beerling et al. 1995). This rhizomatous perennial is an aggressive weed in the British Isles and central and northern Europe where it often forms dense stands along water courses, replacing the native riparian vegetation (Perrins et al. 1992, Brock et al. 1995, de Waal 1995). *P. cuspidatum* was introduced into the United States in the late 1890s as an ornamental, and has been reported from northwestern California, the Pacific Northwest, several north-central and eastern states, and several Canadian provinces (Brock et al. 1995).

TABLE 1. Notes and references related to the occurrence or ecology of selected vascular plant species exotic to North America that were first recorded in the northwestern United States during 1950-1996[1].

Species	Notes	References
Alliaria petiolata	invades woodlands in midwestern and northeastern U.S.	Brothers and Spingarn 1992, Anderson et al. 1996
Anthriscus sylvestris	invades nutrient-rich grasslands in The Netherlands	van Mierlo and van Groenendael 1991
Bryonia alba	spreading rapidly in northwestern U.S.—see text	Mack 1991, Novak and Mack 1995
Butomus umbellatus	aggressively invades wetland habitats	Anderson et al. 1974, Staniforth and Frego 1980
Centaurea montana	escapes from cultivation	
C. virgata	potentially serious grassland invader	Roché and Roché 1989
Chaenorrhinum minus	spreading rapidly in northwestern U.S.	Widrlechner 1983
Crocosmia x crocosmiiflora	reported as a weed in Australia and New Zealand	Johnson 1982, Scott and Delfosse 1992
Crupina vulgaris	probably multiple introductions	Couderc-LeVaillant and Roché 1993, Roché et al. 1997
Epipactis helleborine	one of the few invasive orchids in North America	Brunton 1986
Eragrostis curvula	weed of pasture and conservation areas in Australia	Scott and Delfosse 1992
E. minor	spreading rapidly in northwestern U.S.	
Euphorbia myrsinites	escapes from cultivation	
Heracleum mantegazzianum	escapes from cultivation	Pyšek 1991
Hieracium floribundum	first recorded in northwestern U.S. in 1989	Wilson et al. 1997
H. piloselloides	first recorded in northwestern U.S. in 1988	Wilson et al. 1997
H. pratense	spreading rapidly in northwestern U.S.—see text	Wilson et al. 1997
Hypericum androsaemum	invades pastures and native bushland in Australia	Parsons and Cuthbertson 1992
Impatiens glandulifera[1]	escapes from cultivation, highly invasive—see text	Perrins et al. 1993, Pyšek and Prach 1995
Nardus stricta	reported spreading near Fort Klamath, OR since 1962	
Nicotiana glauca	invasive phreatophyte	Loope et al. 1988, Burgess et al. 1991
Paspalum dilatatum	established along ditches and creek banks in SW Oregon	
Peganum harmala	potentially invasive in semiarid grassland and shrubland	Parsons and Cuthbertson 1992
Pennisetum setaceum	large aggressive bunchgrass	Loope et al. 1988, Burgess et al. 1991
Polygonum cuspidatum	spreading rapidly in northwestern U.S.—see text	Patterson 1976, Beerling et al. 1995, Brock et al. 1995
Prunus avium	widely naturalized; drought tolerant and aggressive	Johnson and Steele 1978
Rosa multiflora	animal-dispersed aggressive shrub; escapes plantings	Patterson 1976, Brothers and Spingarn 1992
Scorzonera laciniata	spreading rapidly in Montana—see text	Brandes 1994, Sivinski et al. 1994
Spartina anglica	invasive in Pacific estuaries	Daehler and Strong 1996
Sisymbrium orientale	present in Arizona by 1931	Burgess et al. 1991
Ventenata dubia	widespread in eastern WA, eastern OR and western ID	

[1]*Impatiens glandulifera* was first collected in Snohomish County, WA, in 1944, but with all subsequent records >1950.



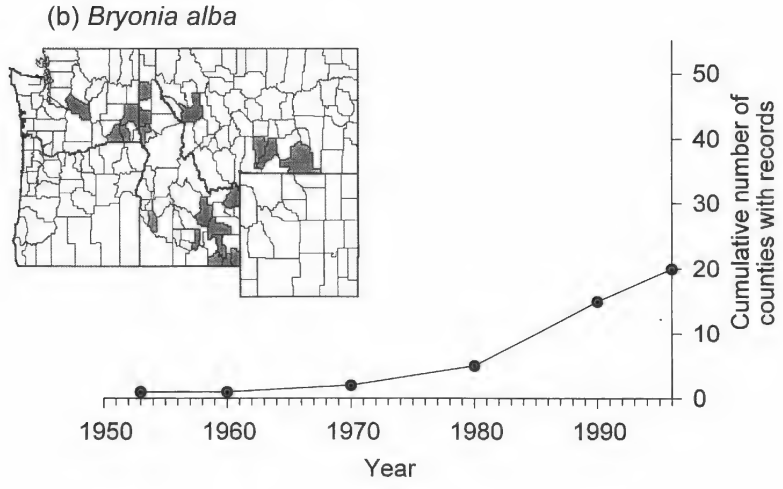
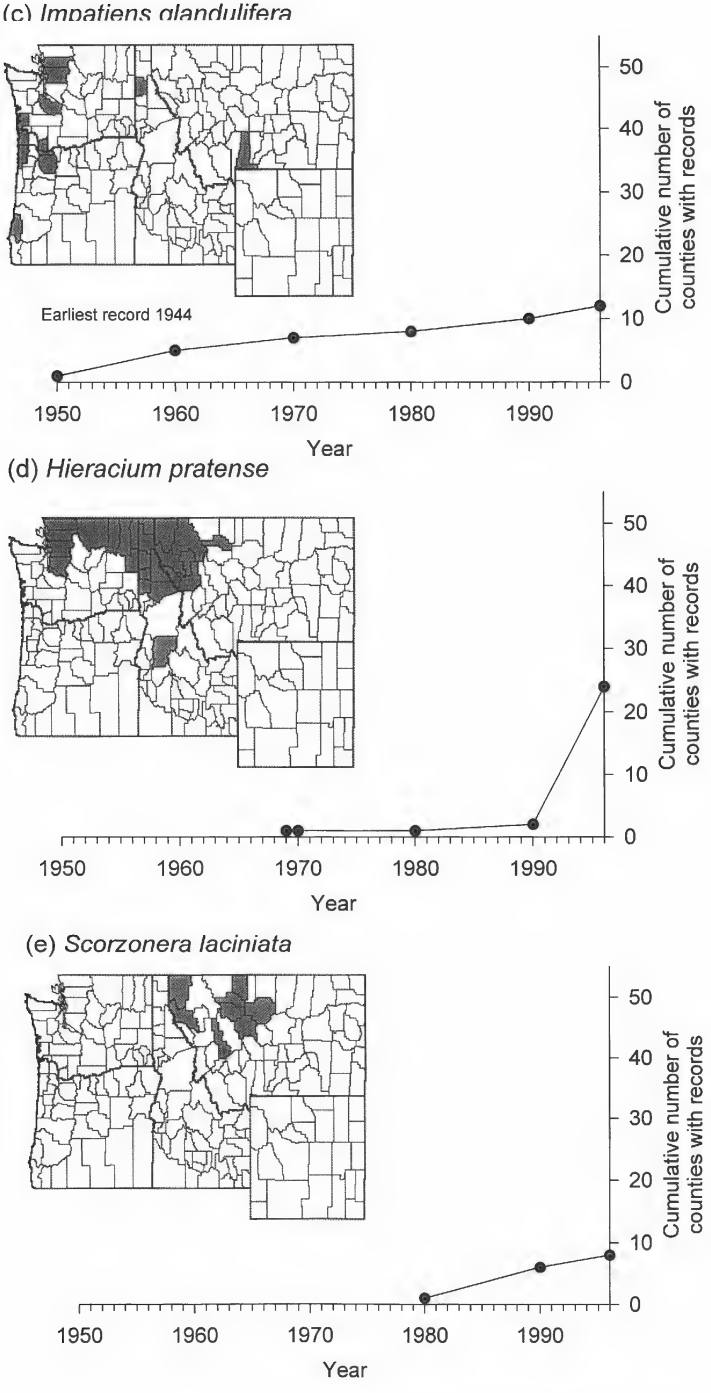


Figure 2. Cumulative number of counties with records for five exotic plant species during 1950-1996. Map insets have shading in counties with distribution records as of 1996. (Continued...)

Figure 2. (Continued)



It has been spreading rapidly in the northwest states since the 1950s (Figure 2a), and has been declared noxious in California, Oregon and Washington. Climate is suitable for *P. cuspidatum* throughout much of the northwest region, but it may be restricted to riparian and other moist habitats due to its requirement for high soil moisture (Beerling et al. 1995). The distribution records suggest that escape from ornamental plantings has contributed to its rapid rate of spread in the northwest states.

White bryony *Bryonia alba* (Cucurbitaceae), a herbaceous perennial vine, has also been spreading rapidly in the northwest United States since the 1950s (Figure 2b). It is native to much of central and eastern Europe and parts of central Asia (Novak and Mack 1995). It was available as an ornamental in the United States as early as 1860, but apparently did not become naturalized until its recent invasion in southeastern Washington, Idaho, Montana and northern Utah (Mack 1991). This invasion probably resulted from 2 or 3 separate introductions (Novak and Mack 1995). It has been reported frequently from riparian habitats and wooded ravines within grassland, sagebrush and ponderosa pine zones. *B. alba* has been declared noxious in Washington.

Himalayan balsam *Impatiens glandulifera* (Balsaminaceae) was first collected in the northwest United States in 1944 in Snohomish Co., Washington (*Gleason 600*, WS), but all subsequent records are >1950. It deserves mention here because of its high invasive potential and continuing range expansion (Figure 2c). *I. glandulifera* is native to the Himalayas and was introduced into Europe as an ornamental in the first half of the 19th century (Perrins et al. 1993, Pyšek and Prach 1995). Its European distribution extends northward to 64° on the east coast of Sweden and correlates with an annual heat sum 2,195 day-degrees (0°C base) (Beerling 1993). It is the tallest annual plant in Europe (up to 2.5 m), and its rapid growth rate and frost tolerance contribute to its strong competitiveness in native communities (Perrins et al. 1993, Pyšek and Prach 1993). In the British Isles and Czech Republic it forms dense stands in damp woodlands and riparian habitats, replacing the native flora (Perrins et al. 1993, Pyšek and Prach 1995). Of the 20 distribution records for *I. glandulifera* in the northwestern U.S., several mention that it had formed large and/or dense colonies in moist habitats such as marshes and ditch banks.

Meadow hawkweed *Hieracium pratense* (Asteraceae) was introduced into the United States as early as 1828, and is now common from Quèbec and Ontario to as far south as Georgia and Tennessee (Wilson et al. 1997). It was first collected in the western U.S. in Pend Oreille County, Washington, in 1969 (*Layser 829*, WS), and has been spreading rapidly in northern Washington, northern Idaho, and northwestern Montana (Figure 2d). The rapid expansion phase probably began earlier than suggested in Figure 2d as most of the post-1990 records resulted from various agency targeted weed surveys. This stoloniferous perennial is native to Europe. It is invasive in mountain meadows and other open habitats in forest zones, as well as in permanent pastures, hayfields and cleared timber units (Wilson et al. 1997). Climate appears suitable for its continued eastward and southeastward expansion throughout much of western Montana and into portions of central Montana (Rice et al. 1997). It has been declared noxious in Washington and Idaho and is proposed for listing in Montana.

False salsify *Scorzonera laciniata* (Asteraceae) was first reported in North America around Boulder, Colorado in the 1950s, and quickly became a locally abundant weed along the foothills of the Front Range (Great Plains Flora Assoc. 1986). It has subsequently spread to Kansas, and has also become a common weed in north and west-central New Mexico (Sivinski et al. 1994). In New Mexico it has been recorded as a weed of lawns and disturbed areas, but also as an adventive component of natural vegetation (Sivinski et al. 1994). The recent records from central and northwest Montana (Figure 2e) similarly note this species occurring in lawns, as well as in disturbed portions of native prairie and in saline habitats near ponds and marshes. Brandes (1994) described its association with saline sites in central Europe, and suggested that the recent strong decline of *S. laciniata* in that region may be due to the coincident decline of salt quarrying which had maintained favorable habitat on tailings. Although its fruits are equipped with a pappus, the effectiveness for long distance dispersal is thought to be minimal because height of the plant is low and the fall rate of fruits is rapid (avg. 53 cm/s, twice that of *Cirsium arvense* fruits) (Brandes 1994). These observations are particularly interesting considering the rapid expansion of *S. laciniata* over a wide portion of the western U.S., and

underscore the relatively greater importance of human-mediated versus natural dispersal mechanisms in large-scale plant invasion (Noble 1989, Panetta and Scanlan 1995).

It should be emphasized that several species recorded recently in the northwest states are exotics well established in other areas of North America that continue to expand their geographic ranges (cf. Rejmánek and Randall 1994). One example is squarrose knapweed *Centaurea virgata*. Not recorded in Oregon until 1988, *C. virgata* was collected in California in 1950 and in Utah in 1954, and was noted anecdotally in Utah as early as 1928 (Roché and Roché 1989). It was estimated to have spread over >20,000 ha in California and Utah as of 1988. The spread of other long-established species into new areas remains a great concern for a number aggressive weeds including *Centaurea diffusa, C. maculosa, C. repens, C. solstitialis, Cytisus scoparius, Echium vulgare, Euphorbia esula, Hypericum perforatum, Isatis tinctoria*, *Linaria dalmatica*, *Lythrum salicaria, Potentilla recta*, *Senecio jacobea,* and *Tamarix* spp.

Composition and Origin of the Recent Exotic Flora

The recently-arrived exotics continue to originate predominantly from Europe and Asia (Table 2). However, the relatively high proportion of perennials and woody growth forms (trees and shrubs) is interesting. The early invaders (mid 1800s - early 1900s) were predominantly herbaceous species, especially annuals (Mack 1986). Time lags between introduction and the beginning of an invasion are generally longer for perennials compared with annuals, and lags may be much longer on average for woody compared with herbaceous growth forms. Lag phases between the first record of occurrence and the beginning of invasion (exponential phase) in central Europe were estimated at 40 years for *Impatiens glandulifera* (annual), 80 years for *Heracleum mantegazzianum* (monocarpic perennial), 46 years for *Polygonum cuspidatum* (polycarpic perennial) and 83 years for *Polygonum sachalinense* (polycarpic perennial) (Pyšek and Prach 1993). Lag phases between the first release for cultivation and the first record from non-cultivated settings averaged 147 years for woody species (131 for shrubs, n=118, and 170 for trees, n=66) introduced in Brandenburg, Germany (Kowarik 1995). Length of the maturation period (time to first reproduction) defines the minimum lag between first introduction and the start of an invasion (Richardson et al. 1994, Kowarik 1995). The timing of subsequent events in the invasion process may be difficult to predict since they are probably determined by complex interactions among life history traits, stochastic environmental factors and genetic plasticity (Richardson et al. 1994, Kowarik 1995, Higgins and Richardson 1996), and socioeconomic factors (Hobbs and Humphries 1995). Nevertheless, Kowarik's (1995) results show that successful invaders do not always begin invasions more rapidly than less successful species. The possibility of long lag phases implies that the number of species invading will continue to increase for a period of time, independently of new introductions.

TABLE 2. Composition and origin of the recent exotic flora of northwest United States.

	Number of species	% of total
Growth form		
Rush	2	1.5
Grass	13	9.8
Forb	86	64
Vine	5	3.8
Shrub	15	11
Tree	12	9.0
Duration		
Annual	37	27
Biennial	5	3.8
Perennial	91	68
Continent(s) of Origin[1]		
Africa	5	3.8
Asia	25	18
Europe	40	30
Eurasia	55	41
South America	4	3.0
South America and Australia	1	0.8
Tropical America, Africa, Asia	1	0.8
interspecific hybrids[2]	2	1.5
Total	133	

[1] Notes: Sources are Bailey et al. (1976), Hultén and Fries (1986), Tutin et al. (1964-80), Hitchcock and Cronquist (1973), Great Plains Flora Assoc. (1986) and Balslev (1980). Several species classified here as ?Eurasian have native ranges extending into northern Africa.

[2] The recent amphiploids *Tragopogon mirus* and *T. miscellus* are considered here to be exotic to North America - see Hitchcock and Cronquist (1973).

Management Implications

Regional-scale management of exotic plant invasions historically has been a reactive effort.

Harmful exotics have often been targeted for expensive control measures only after they became widespread and their negative impacts were apparent. Pro-active management will require greater emphasis on early detection and rapid response to eradicate or contain incipient infestations of potentially harmful species (Westbrooks 1991, Hobbs and Humphries 1995). However, high numbers of exotics continue to establish themselves in the northwest states, and many others are potentially available for escape and naturalization. Predicting which species will invade extensively, and which ecosystems will be affected, remain difficult challenges for plant ecologists. More studies like of those of Scott and Panetta (1993), Pyšek et al. (1995), Tucker and Richardson (1995), Rejmánek (1996), and Reichard and Hamilton (1997) are needed to improve decision guidelines for regulatory screening and prioritization of limited resources for management.

Some limitations on the use of floristic data need to be emphasized (Pyšek 1991). Sampling effort is unevenly distributed in space and time, and many remote areas will not have been sampled at all. The situation is improved some by the availability of Extension Service identification records since the 1950s, which frequently provide occurrence reports from private lands. Herbarium records and agency data more frequently come from public lands including roadsides. A species is more likely to be collected if it is worthy of note from a biogeographical or ecological perspective (such as new state or county records), or for some other property. For example, species with dermaltoxic sap are reported frequently to Extension Service personnel (R. Old, personal communication). A species is more likely to be detected early in the invasion process if it is distinctive and conspicuous (e.g. *Centaurea solstitialis, Heracleum mantegazzianum*). Unequivocal interpretation of floristic data is constrained for taxonomic complexes (*Cardaria, Myriophyllum, Tamarix*, etc.) with a history of misidentification and taxonomic confusion. However, the rapid expansion of a species complex, especially one from a nonnative genus (Rejmánek 1996), is generally indicative of a problem plant.

Floristic databases do offer several clear advances in the management and study of regional-scale plant invasions. They provide ecologists and land managers with easy access to current known distributions of exotic plant species over broad geographical scales. Species lists of relatively new and less well known exotics can be generated for particular sub-regions such as counties, National Forest districts or other multi-county project areas. Increased awareness of these species can enhance early detection of new occurrences. Systematic analysis of the exotic flora in and adjacent to such areas should provide a basis for improved risk assessments of exotic plant invasions. Furthermore, the floristic data can provide information on the species ecology and the types of habitats occupied. Occurrence records can be linked to existing spatial data sets to determine possible correlations with environmental and land use factors (e.g., Sanders 1976, Panetta and Dodd 1987, Sindel and Michael 1992). Reconstructions of the temporal and spatial dynamics of spread are also facilitated by rapid access to the historical distribution data.

Acknowledgements

The INVADERS Database project is supported by the Montana Noxious Weed Trust Fund administered by the Montana Department of Agriculture, with periodic support from the U.S. Forest Service Northern Region. We would like to thank Richard N. Mack, Richard Old, and an anonymous reviewer for providing valuable comments on the manuscript. We also thank Toby Spribille for summarizing and translating parts of Brandes (1994) from German into English. The efforts of numerous plant collectors, both past and present, are gratefully acknowledged.

Literature Cited

Anderson, L. C., C. D. Zeis and S. F. Alam. 1974. Phytogeography and possible origins of *Butomus* in North America. Bull. Torrey Bot. Club 101:292-296.

Anderson, R. C., S. S. Dhillion and T. M. Kelley. 1996. Aspects of the ecology of an invasive plant, garlic mustard (*Alliaria petiolata*), in central Illinois. Restoration Ecol. 4:181-191.

Animal Plant Health Inspect. Serv. 1995. Federal Noxious Weed List. U.S. Dept. Agric., http://www.aphis.usda.gov/ppq/bats.

Bailey, L. H., E. Z. Bailey and the staff of the Liberty Hyde Bailey Hortorium. 1976. Hortus Third. A Concise Dictionary of Plants Cultivated in the United States and Canada. Macmillan, New York.

Baker, H. G. 1986. Patterns of plant invasion in North America. *In* H. A. Mooney and J. A. Drake (eds.). Ecology of Biological Invasions of North America and Hawaii, Springer-Verlag, New York. Pp. 44-57.

Balslev, H. 1980. *Juncus planifolius* (Juncaceae) in North America. Brittonia 32:51-54.

Beck, W. A. and Y. D. Haase. 1989. Historical Atlas of the American West. University of Oklahoma Press, Norman.

Beerling, D. J. 1993. The impact of temperature on the northern distribution limits of the introduced species *Fallopia japonica* and *Impatiens glandulifera* in northwest Europe. J. Biogeogr. 20:45-53.

_____. 1995. General aspects of plant invasions: an overview. *In* P. Pyšek, K. Prach, M. Rejmánek and M. Wade (eds.). Plant Invasions - General Aspects and Special Problems, SPB Academic Publishing, Amsterdam. Pp. 237-247.

Beerling, D. J., B. Huntley and J. P. Bailey. 1995. Climate and the distribution of *Fallopia japonica*: use of an introduced species to test the predictive capacity of response surfaces. J. Veg. Sci. 6:269-282.

Brandes, D. 1994. Verbreitung, ökologie and soziologie von *Scorzonera laciniata* L. in Nordwestdeutschland. Tuexenia 14:415-424.

Brock, J. H. 1994. *Tamarix* spp. (salt cedar), an invasive exotic woody plant in arid and semi-arid riparian habitats of western USA. *In* L. C. de Waal, L. E. Child, P. M. Wade and J. H. Brock (eds.). Ecology and Management of Invasive Riverside Plants, John Wiley & Sons, Chichester. Pp. 27-44.

Brock, J. H., L. E. Child, L. C. de Waal and M. Wade. 1995. The invasive nature of *Fallopia japonica* is enhanced by vegetative regeneration from stem tissues. *In* P. Pyšek, K. Prach, M. Rejmánek and M. Wade (eds.). Plant Invasions—General Aspects and Special Problems, SPB Academic Publishing, Amsterdam. Pp. 131-139.

Brothers, T. S. and A. Spingarn. 1992. Forest fragmentation and alien plant invasion of central Indiana old-growth forests. Conserv. Biol. 6:91-100.

Brunton, D. F. 1986. The helleborine, *Epipactis helleborine* (Orchidaceae), in northern Ontario. Can. Field Nat. 100:127-130.

Burgess, T. L., J. E. Bowers and R. M. Turner. 1991. Exotic plants at the Desert Laboratory, Tucson, Arizona. Madroño 38:96-114.

Campbell, F. T. (ed.). 1997. Worst invasive plant species in continental United States (unpub. list). National Association of Exotic Pest Plant Councils, Springfield, Virginia.

Cheney, R. C. 1983. Names on the Face of Montana. Mountain Press Publishing, Missoula, Montana.

Couderc-LeVaillant, M. and C. T. Roché. 1993. Evidence of multiple introductions of *Crupina vulgaris* in infestations in the western United States. Madroño 40:63-65.

Daehler, C. and D. R. Strong. 1996. Status, prediction and prevention of introduced cordgrass *Spartina* spp. invasions in Pacific estuaries, USA. Biol. Conserv. 78:51-58.

De Waal, L. C. 1995. Treatment of *Fallopia japonica* near water - a case study. *In* P. Pyšek, K. Prach, M. Rejmánek and M. Wade (eds.). Plant Invasions—General Aspects and Special Problems, SPB Academic Publishing, Amsterdam. Pp. 203-212.

Forcella, F. 1985. Final distribution is related to rate of spread in alien weeds. Weed Res. 25:181-191.

Forcella, F. and S. J. Harvey. 1983. Relative abundance in an alien weed flora. Oecologia 59:292-295.

_____. 1988. Patterns of weed migration in northwestern U.S.A. Weed Sci. 36:194-201.

Great Plains Flora Association. 1986. Flora of the Great Plains. University Press of Kansas, Lawrence.

Heywood, V. H. 1989. Patterns, extents and modes of invasions by terrestrial plants. *In* J. A. Drake, H. A. Mooney, F. di Castri, R.H. Groves, F. J. Kruger, M. Rejmánek and M. Williamson (eds.). Biological Invasions: a Global Perspective, John Wiley & Sons, Chichester. Pp. 31-60.

Hickman, J. C. (ed.). 1993. The Jepson Manual. University of California Press, Berkeley.

Higgins, S. I. and D. M. Richardson. 1996. A review of models of alien plant spread. Ecol. Model. 87:249-265.

Hitchcock, C. L. and A. Cronquist. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle.

Hobbs, R. J. and S. E. Humphries. 1995. An integrated approach to the ecology and management of plant invasions. Conserv. Biol. 9:761-770.

Hultén, E. and M. Fries. 1986. Atlas of North European Vascular Plants. Koeltz Sci. Books, Königstein.

Johnson, F. D. and R. Steele. 1978. New plant records for Idaho from Pacific Coastal refugia. Northwest Sci. 52:205-211.

Johnson, P. N. 1982. Naturalised plants in south-west South Island, New Zealand. New Zealand J. Bot. 20:131-142.

Kartesz, J. T. 1994. A Synonymized Checklist of the Vascular Flora of the United States, Canada, and Greenland. Timber Press, Portland, Oregon.

Kowarik, I. 1995. Time lags in biological invasions with regard to the success and failure of alien species. *In* P. Pyšek, K. Prach, M. Rejmánek and M. Wade (eds.). Plant Invasions—General Aspects and Special Problems, SPB Academic Publishing, Amsterdam. Pp. 15-38.

Lesica, P., K. Ahlenslager and J. DeSanto. 1993. New vascular plant records and the increase of exotic plants in Glacier National Park, Montana. Madroño 40:126-131.

Loope, L. L., P. G. Sanchez, P. W. Tarr, W. L. Loope and R. L. Anderson. 1988. Biological invasions of arid land nature reserves. Biol. Conserv. 44:95-118.

Mack, R. N. 1986. Alien plant invasion into the Intermountain West: a case history. *In* H. A. Mooney and J. A. Drake (eds.). Ecology of Biological Invasions of North America and Hawaii, Springer-Verlag, New York. Pp. 191-213.

_____. 1989. Temperate grasslands vulnerable to plant invasions: characteristics and consequences. *In* J. A. Drake, H. A. Mooney, F. di Castri, R.H. Groves, F. J. Kruger, M. Rejmánek and M. Williamson (eds.). Biological Invasions: a Global Perspective, John Wiley & Sons, Chichester. Pp. 155-179.

_____. 1991. The commercial seed trade: an early disperser of weeds in the United States. Econ. Bot. 45:257-273.

Noble, I. R. 1989. Attributes of invaders and the invading process: terrestrial and vascular plants. *In* J. A. Drake, H. A. Mooney, F. di Castri, R.H. Groves, F. J. Kruger, M. Rejmánek and M. Williamson (eds.). Biological Invasions: a Global Perspective, John Wiley & Sons, Chichester. Pp. 301-313.

Novak, S. J. and R. N. Mack. 1995. Allozyme diversity in the apomictic vine *Bryonia alba* (Cucurbitaceae): potential consequences of multiple introductions. Am. J. Bot. 82:1153-1162.

Panetta, F. D. and J. Dodd. 1987. Bioclimatic prediction of the potential distribution of skeleton weed *Chondrilla juncea* L. in western Australia. J. Aust. Inst. Agric. Sci. 53:11-16.

Panetta, F. D. and J. C. Scanlan. 1995. Human involvement in the spread of noxious weeds: what plants should be declared and when should control be enforced? Plant Prot. Quart. 10:69-74.

Parsons, W. T. and E. G. Cuthbertson. 1992. Noxious Weeds of Australia. Inkata Press, Melbourne.

Patterson, D. T. 1976. The history and distribution of five exotic weeds in North Carolina. Castanea 41:177-180.

Perrins, J., A. Fitter and M. Williamson. 1993. Population biology and rates of invasion of three introduced *Impatiens* species in the British Isles. J. Biogeogr. 20:33-44.

Perrins, J., M. Williamson and A. Fitter. 1992. A survey of differing views of weed classification: implications for regulation of introductions. Biol. Conserv. 60:47-56.

Pyšek, P. 1991. *Heracleum mantegazzianum* in the Czech Republic: dynamics of spreading from the historical perspective. Folia Geobot. Phytotax. 26:439-454.

_____. 1995. On the terminology used in plant invasion studies. *In* P. Pyšek, K. Prach, M. Rejmánek and M. Wade (eds.). Plant Invasions—General Aspects and Special Problems, SPB Academic Publishing, Amsterdam. Pp. 71-81.

Pyšek, P. and K. Prach. 1993. Plant invasions and the role of riparian habitats: a comparison of four species alien to central Europe. J. Biogeogr. 20:413-420.

_____. 1995. Invasion dynamics of *Impatiens glandulifera*—a century of spreading reconstructed. Biol. Conserv. 74:41-48.

Pyšek, P., K. Prach and P. Šmilauer. 1995. Relating invasion success to plant traits: an analysis of the Czech alien flora. *In* P. Pyšek, K. Prach, M. Rejmánek and M. Wade (eds.). Plant Invasions—General Aspects and Special Problems, SPB Academic Publishing, Amsterdam. Pp. 39-60.

Randall, J. M. and J. Marinelli (eds). 1996. Invasive Plants. Weeds of the Global Garden. Brooklyn Botanic Garden, Brooklyn, NY.

Reichard, S. H. and C. W. Hamilton. 1997. Predicting invasions of woody plants introduced into North America. Conserv. Biol. 11:193-203.

Rejmánek, M. 1996. A theory of seed plant invasiveness: the first sketch. Biol. Conserv. 78:171-181.

Rejmánek, M. and J. M. Randall. 1994. Invasive alien plants in California: 1993 summary and comparison with other areas in North America. Madroño 41:161-177.

Rice, P. M. 1991. Sulfur cinquefoil: a new threat to biological diversity. West. Wildlands 17(2):34-40.

_____. 1998. INVADERS Database Release 6.5. Division of Biological Sciences, The University of Montana, Missoula. http://invader.dbs.umt.edu.

Rice, P. M., J. C. Toney, R. Sacco and D. Cooksey. 1997. Climatic correlations and predicted potential ranges of species in the Montana Weed Seed Free Forage Program: first approximations. Final Report, Coop. Agric. Pest Survey, Dept. Plant & Soil Sci., Montana State Univ., Bozeman. 156 pp.

Richardson, D. M., P. A. Williams and R. J. Hobbs. 1994. Pine invasions in the Southern Hemisphere: determinants of spread and invadability. J. Biogeogr. 21:511-527.

Roché, C. T. and B. F. Roché, Jr. 1989. Introductory notes on squarrose knapweed (*Centaurea virgata* Lam. ssp. *squarrosa* Gugl.). Northwest Sci. 63:246-252.

Roché, C. T., D. C. Thill and B. Shafii. 1997. Prediction of flowering in common crupina (*Crupina vulgaris*). Weed Sci. 45:519-528.

Sanders, R. W. 1976. Distributional history and probable ultimate range of *Galium pedomontanum* (Rubiaceae) in North America. Castanea 41:73-80.

Scott, J. K. and E. S. Delfosse. 1992. Southern African plants naturalized in Australia: a review of weed status and biological control potential. Plant Protect. Quart. 7:70-80.

Scott, J. K. and F. D. Panetta. 1993. Predicting the Australian weed status of southern African plants. J. Biogeogr. 20:87-93.

Sheley, R. L. (ed.). 1994. The identification, distribution, impacts, biology and management of noxious range weeds. Contract Order #43-0E00-4-915, USDA Eastside Ecosystem Management Project, Walla Walla, Washington. 366 pp.

Sindel, B. M. and P. W. Michael. 1992. Spread and potential distribution of *Senecio madagascariensis* Poir. (fireweed) in Australia. Aust. J. Ecol. 17:21-26.

Sivinski, R., T. Lowrey and R. Peterson. 1994. Additions to the native and adventive flora of New Mexico. Phytologia 76:473-479.

Staniforth, R. J. and K. A. Frego. 1980. Flowering rush (*Butomus umbellatus*) in the Canadian Prairies. Can. Field Nat. 94:333-336.

Tucker, K. C. and D. M. Richardson. 1995. An expert system for screening potentially invasive alien plants in South African fynbos. J. Environ. Manage. 44:309-338.

Tutin, T. G., V. H. Heywood, N. A. Burges, D. H. Valentine, S. M. Walters, D. A. Webb (eds). 1964-80. Flora Europaea, volumes 1-5. Cambridge Univ. Press, Cambridge.

Usher, M. B. 1988. Biological invasions of nature reserves: a search for generalisations. Biol. Conserv. 44:119-135.

van Mierlo, J. E. M. and J. M. van Groenendael. 1991. A population dynamic approach to the control of *Anthriscus sylvestris* (L.) Hoffm. J. Appl. Ecol. 28:128-139.

Vitousek, P. M., C. M. D'Antonio, L. L. Loope and R. Westbrooks. 1996. Biological invasions as global environmental change. Am. Sci. 84:468-478.

Westbrooks, R. 1991. Plant protection issues. I. A commentary on new weeds in the United States. Weed Technol. 5:232-237.

Widrlechner, M. P. 1983. Historical and phenological observations on the spread of *Chaenorrhinum minus* across North America. Can. J. Bot. 61:179-187.

Received 20 December 1997
Accepted for publication 14 July 1998

Wilson, L. M., J. P. McCaffrey, P. C. Quimby, Jr., and J. L. Birdsall. 1997. Hawkweeds in the northwestern United States. Rangelands 19(4):18-23.

Yates, R. and C. Yates. 1987. Washington State Atlas. 1987 Revised Edition. The Information Press, Eugene, Oregon.

APPENDIX. One hundred thirty-three exotic vascular plant species first reported during 1950-1996[1] in the five-state region of Washington, Oregon, Idaho, Montana and Wyoming, determined by query of the INVADERS Database Release 6.5. The number of counties with records as of 1996 is based 199 counties in the five states. See **Methods** for the definitions of terms used to describe ecological status. Presence on state or provincial noxious weed lists (any category) is indicated for the five-state region and adjacent states and provinces (and Fed. for 2 species on the federal noxious weed list).

Species	Earliest record	No. counties with records	Regions with records[2]	Ecological status	Regulatory status
Aegopodium podagraria L.	1959	14	WWA, EWA, WOR, EOR, SID, WMT	Localized	
Ajuga reptans L.	1970	5	WWA, EWA, WOR	Localized	
Alchemilla vulgaris L.	1975	2	WOR, WMT	Established	
Alliaria petiolata (Bieb.) Cavara & Grande	1959	1	Multnomah Co., OR	Established	
Alopecurus arundinaceus Poir.	1963	9	EWA, NID, WMT, EMT, WWY	Invasive	
Anchusa barrelieri (All.) Vitman	1991	1	Whatcom Co., WA	Established	
Anthriscus sylvestris (L.) Hoffm.	1985	7	WWA, EWA, NID	Invasive	WA
Atriplex heterosperma Bunge	1953	19	WWA, EWA, NID, WMT, EMT, EWY	Invasive	
Atriplex oblongifolia Waldst & Kit.	1966	1	Toole Co., MT	Established	
Barbarea verna (Mill.) Asch.	1986	2	WOR, WMT	Established	
Bidens pilosa L.	1993	1	Lake Co., OR	Unknown	
Bryonia alba L.	1953	20	EWA, NID, SID, WMT, EMT	Invasive	WA
Butomus umbellatus L.	1956	5	NID, SID, WMT	Invasive	
Campanula glomerata L.	1958	19	WWA, EWA, NID, SID, WMT, EMT	Localized	
Carthamus baeticus (Boiss. & Reut.) Lara	1987	1	Jackson Co., OR	Established	OR, CA
Carthamus tinctorius L.	1957	24	WWA, EWA, WOR, NID, SID, WMT, EMT	Invasive	
Centaurea dealbata Willd. Per.	1988	3	WWA, WMT, EMT	Localized	
Centaurea montana L.	1960	6	WWA, EWA, WOR, SID, WMT	Localized	
Centaurea trichocephala Bieb. *ex* Willd.	1983	1	Yakima Co., WA	Established	
Centaurea virgata Lam.	1988	5	WOR, EOR	Invasive	OR, CA, CO, UT
Centranthus ruber (L.) DC.	1970	6	WWA, EWA, WOR	Established	
Cerastium dubium (Bast.) O. Schwarz.	1981	5	WWA, EOR, SID	Invasive	
Cerastium siculum Guss.	1969	5	EWA, EOR	Invasive	
Chaenorrhinum minus (L.) Lange	1976	9	EWA, EOR, NID, WMT	Invasive	WA
Chelidonium majus L.	1955	3	WWA, EWA, WMT	Established	
Coronilla varia L.	1951	12	EWA, WOR, SID, WMT	Invasive	
Cotoneaster franchetti Bois.	1977	1	Lewis Co., WA	Unknown	
Cotoneaster lacteus W. W. Smith	1993	1	Polk Co., OR	Unknown	
Crataegus monogyna Jacq.	1966	5	WWA, WOR	Established	
Crepis tectorum L.	1983	4	EWA, WOR, WMT, EMT	Localized	AB
Crocosmia x crocosmiiflora (V. Lemoine *ex* E. Morr) N. E. Br.	1983	1	Lincoln Co., OR	Established	
Crucianella angustifolia L.	1991	1	Clearwater Co., ID	Established	
Crupina vulgaris Cass.	1969	6	WWA, EOR, NID	Invasive	ID, OR, MT, WA, BC, CA, Fed
Cryptomeria japonica (L. F.) D. Don	1953	3	WWA, WOR, EOR	Unknown	

Species	Earliest record	No. counties with records	Regions with records[2]	Ecological status	Regulatory status
Cunninghamia lanceolata (Lamb.) Hook.	1987	3	WOR	Unknown	
Cymbalaria muralis E. Mey & Scherb.	1988	3	EWA, WOR	Unknown	
Cynara cardunculus L.	1968	2	WWA, WOR	Localized	CA
Cytisus monspessulanus L.	1988	1	Coos Co., OR	Established	OR, CA
Daphne mezereum L.	1969	3	EWA, WOR, WMT	Unknown	
Delphinium consolida L.	1995	2	Gallatin Co., MT	Established	
Dioscorea batatas Decene.	1990	1	Union Co., OR	Unknown	
Echinops ruthenicus Bieb.	1954	5	EWA, WMT	Established	
Echinops sphaerocephalus L.	1990	2	EWA, EOR	Established	
Eichhornia crassipes (Mart.) Solms-Laub	1996	1	Cowlitz Co., WA	Established	
Elymus junceus Fisch.	1951	11	WMT, EMT	Invasive	
Epilobium hirsutum L.	1984	2	WWA	Established	
Epipactis helleborine (L.) Crantz	1985	3	WOR, WMT	Established	
Eragrostis curvula (Schrad.) Nees	1990	2	WOR, EOR	Established	
Eragrostis minor Host	1984	9	EWA, EOR, NID, SID, WMT	Invasive	
Euonymus fortunei (Turcz.) Hand.-Mazz.	1980	2	WWA, SID	Unknown	
Euphorbia lathyris L.	1991	9	WWA, EWA, WOR, EOR	Established	
Euphorbia myrsinites L.	1977	22	WWA, EWA, WOR, EOR, NID, SID	Invasive	CO
Forsynthia suspensa (Thunb.) Vahl	1980	2	WWA, EMT	Established	
Fumaria parviflora Lam.	1992	1	Baker Co., OR	Established	
Galium pedemontanum (Bellardi) All.	1974	4	NID, WMT	Invasive	
Geum urbanum L.	1970	2	EWA, WOR	Established	
Glaucium corniculatum (L.) J.H. Rudolph	1964	1	Stillwater Co., MT	Invasive	
Gypsophila elegans Bieb.	1995	1	Minidoka Co., ID	Unknown	
Halimodendron halodendron (Pallas) Voss	1995	1	Broadwater Co., MT	Established	CA
Hemerocallis fulva L.	1978	2	SID, WMT	Established	
Heracleum mantegazzianum Somm. & Levier	1962	8	WWA, EWA, WOR	Established	WA, Fed
Hieracium floribundum Wimmer & Grab	1989	4	WWA, NID, WMT	Invasive	
Hieracium piloselloides Vill.	1988	2	WWA, WMT	Invasive	
Hieracium pratense L.	1969	24	WWA, EWA, NID, SID, WMT	Invasive	ID, WA
Hieracium vulgatum Fries	1960	2	WWA, WOR	Established	
Hordeum distichon L.	1976	4	EWA, SID, EMT, WWY	Established	
Hypericum androsaemum L.	1983	4	WWA, WOR	Localized	
Hypochaeris glabra L.	1978	1	Curry Co., OR	Established	
Impatiens balfouri Hook.	1970	4	WWA, WOR	Unknown	
Impatiens glandulifera Royle	1944	12	WWA, WOR, NID, WMT	Invasive	
Juncus compressus Jacq.	1979	2	EWY	Established	
Juncus planifolius R. Br.	1969	2	WOR	Established	
Kickxia spuria (L.) Dumort.	1956	5	WOR, WMT	Invasive	
Koelreuteria paniculata Laxm.	1987	4	WOR, SID	Unknown	
Lamium hybridum Vill.	1956	2	WOR	Localized	WA
Lepyrodiclis holosteoides Fenzl.	1986	2	EWA, NID	Invasive	WA

Species	Earliest record	No. counties with records	Regions with records[2]	Ecological status	Regulatory status
Ligustrum japonicum Thunb.	1981	1	Benton Co., WA	Unknown	
Ligustrum sinense Lour.	1990	2	WOR	Unknown	
Lonicera etrusca Santi	1988	2	WOR	Established	
Lonicera maackii (Rupr.) Maxim.	1994	1	Ada Co., ID	Unknown	
Lonicera nitida E. H. Wils.	1957	4	WOR	Localized	
Lychnis dioica (L.) Clairv.	1961	4	WWA, WOR, WMT	Established	
Lythrum virgatum L.	1990	1	Phillips Co., MT	Unknown	MT, WA, ND
Milium vernale Bieb.	1987	2	NID	Invasive	ID
Nardus stricta L.	1962	1	Klamath Co., OR	Invasive	ID, OR
Nicotiana glauca Graham	1968	1	Spokane Co., WA	Unknown	
Origanum vulgare L.	1975	6	EWA, WOR, EOR, NID, SID	Localized	
Ornithogalum nutans L.	1991	1	Linn Co., OR	Invasive	
Paspalum dilatatum Poir.	1979	4	WOR	Invasive	
Paulownia tomentosa (Thunb.) Steud.	1984	4	WWA, WOR	Unknown	
Peganum harmala L.	1967	4	EWA, EOR, EMT	Invasive	OR, WA, CA, CO, NV
Pennisetum setaceum (Forssk.) Chiov.	1982	2	WOR	Unknown	
Picris echioides L.	1978	3	WOR, WMT	Unknown	
Picris hieracioides L.	1981	2	WWA	Invasive	WA
Polygala vulgaris L.	1994	1	Coos Co., OR	Localized	
Polygonum aubertii Litt.	1967	3	WWA, EWA	Unknown	
Polygonum cuspidatum Siebold. & Zucc.	1957	52	WWA, EWA, WOR, NID, SID, WMT, EMT	Invasive	OR, WA, CA
Prunus armeniaca L.	1974	6	EOR, NID, SID, EMT	Invasive	
Prunus avium L.	1957	9	WWA, EWA, WOR, NID	Invasive	
Prunus padus L.	1973	6	WWA, WMT, EMT	Unknown	
Prunus persica (L.) Batsch.	1978	2	NID, SID	Unknown	
Prunus tomentosa Thunb.	1965	25	WWA, EWA, WOR, EOR, SID, WMT, EMT	Unknown	
Ranunculus ficaria L.	1988	1	Multnomah Co., OR	Established	
Ranunculus parviflorus L.	1983	3	WOR	Established	
Rhamnus frangula L.	1992	1	Ada Co., ID	Unknown	
Rorippa austriaca (Crantz) Bess.	1969	6	EWA, SID, WMT	Invasive	WA, CA, NV
Rosa multiflora Thunb. *ex* Murr.	1984	1	Polk Co., OR	Established	
Rumex sanguineus L.	1978	2	WOR, WMT	Established	
Salix babylonica L.	1953	3	EOR, NID, WMT	Established	
Salix pentandra L.	1957	2	WMT	Unknown	
Salsola collina Pallas	1961	5	WMT, EMT, EWY	Established	CA, CO, SK
Saponaria ocymoides L.	1956	4	WWA, WOR, EOR	Invasive	
Satureja acinos (L.) Scheele	1983	2	NID, WMT	Established	
Scorzonera hispanica L.	1984	1	Pondera Co., MT	Localized	
Scorzonera laciniata L.	1980	8	WMT	Invasive	
Senecio mikanioides Otto.	1976	1	Richland Co., MT	Unknown	
Senecio viscosus L.	1991	1	Boundary Co., ID	Localized	
Sisymbrium orientale L.	1973	1	Lane Co., OR	Established	
Sorghum almum Parodi	1961	1	Multnomah Co., OR	Established	UT
Sorghum sudanense (Piper.) Stapf.	1983	3	WWA, EWA, WOR	Established	
Spartina anglica C.E. Hubbard	1983	1	Island Co., WA	Invasive	WA
Thalictrum aquilegifolium L.	1953	2	WWA, WOR	Localized	
Thesium linophyllon L.	1992	1	Madison Co., MT	Invasive	

Species	Earliest record	No. counties with records	Regions with records[2]	Ecological status	Regulatory status
Tragopogon mirus Ownbey	1951	3	WWA, WMT	Established	
Tragopogon miscellus Ownbey	1957	7	EWA, NID, WMT, EWY	Invasive	
Trifolium resupinatum L.	1991	1	Linn Co., OR	Localized	
Tussilago farfara L.	1991	1	Jefferson Co., WA	Localized	
Ulmus parvifolia Jacq.	1974	1	Franklin Co., WA	Unknown	
Ventenata dubia (Leers) Coss. & Dur.	1957	14	WWA, EWA, WOR, EOR, NID, SID	Invasive	
Verbascum virgatum Stokes	1986	1	Bannock Co., ID	Established	
Veronica triphyllos L.	1961	4	EWA, EOR	Invasive	
Veronica verna L.	1961	10	EOR, NID, WMT	Invasive	
Vitis vinifera L.	1974	4	WWA, EWA, NID	Established	

[1]*Impatiens glandulifera* was first collected in Snohomish County, WA, in 1944, but with all subsequent records >1950.

[2]County names are given for species with records from a single county. For species with records from >1 county, the following region codes are used: WWA (western Washington), EWA (eastern Washington), WOR (western Oregon), EOR (eastern Oregon), NID (northern Idaho), SID (southern Idaho), WMT (western Montana), EMT (eastern Montana), WWY (western Wyoming) and EWY (eastern Wyoming).

Jeffrey D. Grizzel and **Noel Wolff,** Washington Department of Natural Resources 919 North Township Street, Sedro-Woolley, WA 98284

Occurrence of Windthrow in Forest Buffer Strips and its Effect on Small Streams in Northwest Washington

Abstract

Retaining streamside buffers has become a common way of protecting streams during timber harvest operations. Trees within forest buffers help stabilize streambanks, provide shade, and serve as a source of large woody debris. However, buffer trees are often subject to increased levels of windthrow which may impair some buffer functions. Forty (40) forest buffers bordering small, non-fish bearing streams in northwest Washington were assessed to quantify the level and in-stream effects of windthrow 1 to 3 years after clearcut harvest of adjacent timber. On average, windthrow affected 33 percent of buffer trees and ranged from 2 to 92 percent across the 40 sites. Sixty-seven percent of windthrown trees fell to the north, northeast, or northwest, while only three percent of the total fell towards the south. Large woody debris present in streams at the time of harvest was significantly larger than debris recruited as a result of buffer windthrow (t-test; $p<0.01$). Windthrow increased total in-stream large woody debris piece counts by 52 percent. Seventy-five percent of in-stream large woody debris pieces recruited to streams post-harvest were suspended above the bankfull channel while four percent stored sediment. Seventeen percent of uprooted trees delivered sediment to stream channels. The average volume input was 0.16 cubic meters per uprooted tree and 0.48 cubic meters per 100 meters of stream channel at 39 sites where mass wasting did not occur. At most sites, the volume of sediment input to streams was small relative to the amount stored behind obstructions. Large woody debris was the primary component of 93 percent of in-stream obstructions which stored sediment.

Introduction

Tree mortality resulting from windthrow (uprooting and stem breakage) has been a concern to forest land managers in the Pacific Northwest for most of this century. From a timber production perspective, windthrown trees represent an economic loss. These trees lose commercial value rapidly and salvage operations are often costly. Additionally, if not salvaged, insects attracted to the dead trees can spread into surrounding timber. From a broader ecological perspective, windthrow is a natural occurrence, and downed trees contribute to forest and stream productivity.

Since the 1970s, the establishment of forest buffers has increasingly become a way of protecting streams during timber harvest operations. A common rationale for retaining streamside buffers is the assumption that they can provide many of the same functions as an intact forest. However, trees within buffers are subject to increased wind exposure and significant amounts of windthrow can impair some buffer functions. The net effect of windthrow on streams is often debated from water quality, fish habitat, channel morphology and legal liability perspectives.

State and private forest land managers in northwest Washington have established buffers which exceed state Forest Practice rules on many small, non-fish bearing streams during the past several years. Instances of severe windthrow in these buffers have caused managers to question the practice of retaining "non-required" buffers. This study was undertaken to develop quantitative information regarding the fate and function of second-growth forest buffers retained along small, non-fish-bearing streams.

Published studies dating from the 1950s document a wide array of site, tree and forest stand characteristics that influence windthrow occurrence in Pacific Northwest forests. Regrettably, data are lacking to support the cause-and-effect relationships reported by many of those studies (Rollerson 1982). Early windthrow studies in Washington and Oregon focused on mortality along clearcut harvest boundaries and offered recommendations for cutting-line placement to reduce windthrow (Ruth and Yoder 1953; Gratkowski 1956; Steinbrenner and Gessel 1956). Research emphasis on windthrow shifted to streamside buffers in the 1970s as buffers became more common on public and private forest lands (Moore 1977; Hobbs and Halbach 1981; Steinblums et al. 1984; Andrus and Froehlich 1988; Sherwood 1993; Timber, Fish and Wildlife 1994; Mobbs and Jones 1995).

© 1998 by the Northwest Scientific Association. All rights reserved.

Streamside trees can exert significant influence on channel morphology and fluvial processes in small, low-order streams of the Pacific Northwest (Naiman et al. 1992). Standing trees and/or their root systems help retard streambank erosion and maintain stability of stream-adjacent hillslopes (Sullivan et al. 1987). Fallen trees and limbs supply in-stream woody debris which helps store sediment, dissipate streamflow energy, and create channel complexity. Despite these positive effects of woody debris on channel morphology, our understanding of the role of riparian and stream-adjacent forests in supplying wood has developed only recently (Bisson et al. 1987).

In this study, we characterized tree condition, large woody debris function, and stream sediment input and storage within forty (40) streamside buffers and associated non-fish bearing streams 1 to 3 years following clearcut harvest of adjacent second-growth timber. The objectives of this study were to:

1) quantify the amount and type of tree windthrow by species;

2) assess the abundance and function of in-stream large woody debris;

3) quantify the volume of in-stream sediment stored in discrete accumulations or wedges and the volume of sediment delivered to stream channels from uprooted trees.

Methods

Site Selection

State and private forest land managers were asked to identify potential study buffers adjacent to small streams on the lower, west slope of the North Cascades within the Stillaguamish, Skagit and Nooksack river basins of northwest Washington. From these potential sites, we randomly selected 40 buffers that met the following criteria:

1) non-fish bearing stream >1 meter average width;

2) buffer had a continuous, 180 meter or longer reach within the harvest unit;

3 clearcut harvest of adjacent timber occurred during the previous three years;

4) buffer trees were retained on both sides of the stream.

While the large majority of buffers had no removal of live trees, harvest of selected larger conifer trees did occur at three sites. The buffers were typical of merchantable, second-growth forest stands in northwest Washington, ranging in age from 40 to 60 years.

Inventory Procedure

Field work was completed during the summer of 1996. Data were collected within a 150 meter reach randomly located within each buffer. Total buffer length rarely exceeded 300 meters, thus the study reach usually included at least half of the total buffer length (≥50% sample).

Each study reach was divided into 15 meter segments. Channel gradient was measured for each segment; bankfull channel width, buffer width (slope distance), and adjacent hillslope gradients were measured at each segment node (11 locations). Buffer width and hillslope gradients were measured perpendicular to stream orientation. The "forming structure" associated with each in-stream sediment wedge was determined and stored sediment volume was estimated based on surface area and step height. Four classes of forming structures were identified: (1) pre-harvest large woody debris, (2) post-harvest large woody debris, (3) combination of pre- and post-harvest large woody debris, or (4) bedrock and/or boulder.

In-stream large woody debris >10 centimeters in diameter and >1.5 meters in length was tallied. Hydraulic function (sediment storage, bank protection, bank erosion, channel roughness, or bridging) and time-of-entry (pre- or post-harvest) was recorded for each piece lying within the vertical projection of the bankfull channel. Woody debris pieces outside this zone (i.e., on adjacent hillslopes) were not included in the inventory. Post-harvest debris pieces were differentiated from pre-harvest pieces based primarily on physical condition. It was assumed that pieces in more advanced stages of decay had been recruited to the channel prior to harvesting, while pieces with intact bark and/or foliage were of post-harvest origin (i.e., 1 to 3 years since time of recruitment). In addition, the degree of embeddedness exhibited by a particular piece was often used as an indicator of recruitment timing.

All standing, uprooted, and broken trees 15 centimeters diameter at breast height (DBH) and larger were inventoried. Downed trees that

appeared to result from windthrow prior to timber harvest were not inventoried. Such trees were typically in a more advanced state of decay as evidenced by loose or missing bark, and loss of branches and/or foliage. Tree condition, (standing, uprooted, or broken), diameter at breast height (DBH), distance from channel and where applicable, direction of fall, was measured. The area downslope of each uprooted tree was examined for evidence of sediment delivery to the stream channel. Where sediment delivery occurred, the volume was estimated based on surface area and depth of exposed root mass and evidence of soil movement to the channel.

Results

Site Characteristics

Most study streams exhibited morphologies typical of step-pool or cascade channel types as described by Montgomery and Buffington (1993). Streams were generally small, averaging less than 3 meters in bankfull width (Table 1). Channel gradients varied considerably and averaged 24 percent (Table 1). The outer edges of buffers often corresponded with distinct topographic slope breaks. Total buffer widths (both sides of stream) averaged 26 meters while hillslope gradients averaged 39 percent (Table 1). Sites with lower gradient channels and adjacent hillslopes were usually located in relatively wide valley bottoms while sites with steeper channels and adjacent hillslopes tended to be at higher elevations in midslope topographic positions.

The number of trees inventoried within buffer sites ranged from 60 to 537. Variations in the number of trees inventoried were attributable to differences in buffer width and stand density between sites. Stand densities prior to harvest averaged 507 trees/hectare or 47.4 m^2 basal area/hectare (Table 1). Conifer species comprised at least 75 percent of stand density (number of trees and basal area) at 19 of the 40 sites and 90 percent or more at 14 sites. Tree DBH averaged 32.9 centimeters (Table 1).

The most common species was western hemlock (*Tsuga heterophylla*), which accounted for 33 percent of all trees inventoried. Western redcedar (*Thuja plicata*), red alder (*Alnus rubra*), and Douglas-fir (*Pseudotsuga menziesii*) accounted for 22 percent, 20 percent, and 10 percent of all trees, respectively. Bigleaf maple (*Acer macrophyllum*), Pacific silver fir (*Abies amabilis*), Alaska yellow cedar (*Chamaecyparis nootkatensis*), and black cottonwood (*Populus trichocarpa*) comprised the remaining 15 percent of trees inventoried.

Windthrow

Windthrow averaged 33 percent of stand density across the 40 sites (Figure 1). This was true regardless of whether windthrow was calculated as a proportion of total stems (trees/ha) or as a proportion of total basal area (m^2/ha). Uprooting was the more common form of windthrow, averaging 27 percent of stand density while breakage accounted for the remaining six percent (Figure 1). One-third or less of the trees were windthrown at 24 sites while more than two-thirds of the trees were windthrown at three sites.

The level of windthrow varied among tree species. Pacific silver fir and western hemlock experienced the highest levels of windthrow at 37.3 and 36.0 percent of total stems, respectively. Bigleaf maple was least subject to windthrow, with 7.5 percent of trees being uprooted or broken. Windthrow occurred at intermediate levels for red

TABLE 1. Characteristics of 40 forest buffers and associated non-fish-bearing streams in northwest Washington: channel width (average channel width), buffer width (average buffer width on both sides of stream), channel gradient (average channel gradient), hillslope gradient (average hillslope gradient, both sides of stream), stand density (stand density, expressed as trees/hectare and m^2 basal area/ha; includes standing, uprooted, and broken trees), and stand diameter at breast height (average diameter, includes standing, uprooted and broken trees).

	Channel Width (m)	Buffer Width (m)	Channel Gradient (%)	Hillslope Gradient (%)	Density (trees/ha)	Stand Basal Area (m^2/ha)	DBH (cm)
Mean	2.7	26.3	24	39	484	47.4	32.9
Min	1.4	8.5	1	3	261	20.0	24.1
Max	5.7	64.9	63	75	995	87.3	50.0
S.D.	1.0	13.9	15	18	160	13.0	5.2

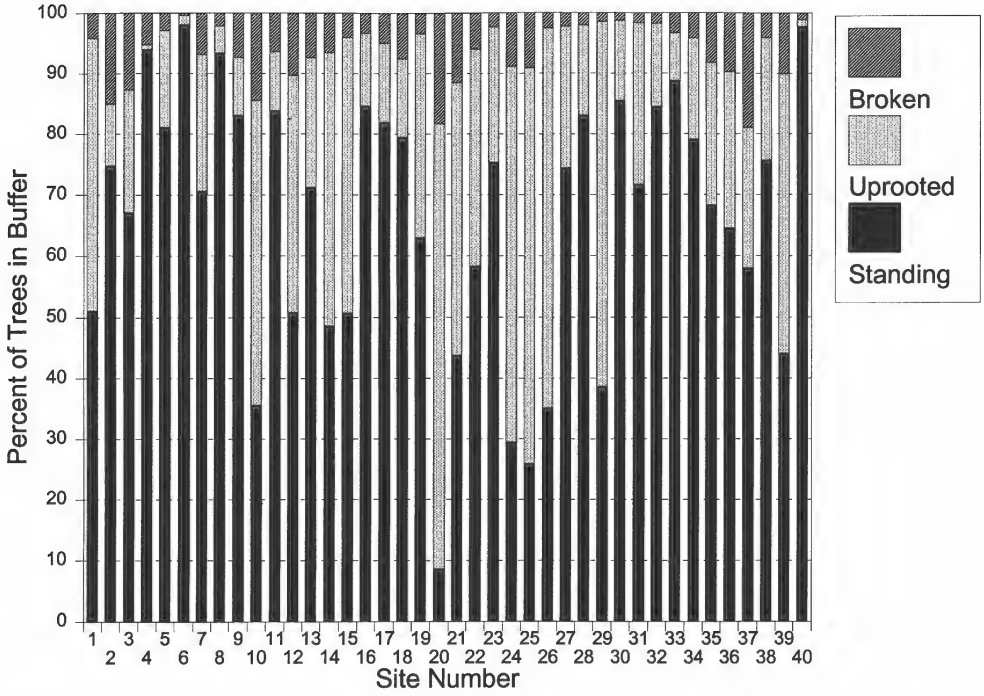


Figure 1. Proportion of standing, uprooted, and broken trees in 40 forest buffers in northwest Washington (each bar represents one site).

alder (17.2 percent), Douglas-fir (20.2 percent), and western redcedar (21.8 percent). Relatively high levels of windthrow for Pacific silver fir and western hemlock were documented in both mixed species stands as well as stands dominated by these species.

Average diameters of windthrown trees were significantly greater than standing trees for four of the six most common species ($p<0.01$, Table 2). Windthrown western redcedar, red alder, Douglas-fir, and Pacific silver fir tended to be larger than standing trees of the same species while no difference between windthrown and standing trees existed for western hemlock and bigleaf maple.

The direction of fall of windthrown trees was strongly influenced by prevailing southerly winds. While 67 percent of all windthrown trees fell to the north, northeast, or northwest, only three percent of the total fell towards the south (Figure 2). This pattern seems to be independent of stream/buffer orientation since the 40 sites were fairly evenly distributed with respect to the four cardinal directions (10 sites were oriented north-south, 8 were oriented northeast-southwest, 10 were oriented east-west, and 12 were oriented northwest-southeast).

In-Stream Large Woody Debris

Approximately one-third of all in-stream large woody debris pieces entered the stream following adjacent clearcut harvest. The proportion of post-harvest debris within the bankfull channel ranged from 2 to 77 percent of total pieces across the 40 sites. Post-harvest large woody debris comprised 25 percent of total woody debris pieces at 16 sites and 50 percent at seven sites. Piece frequencies averaged 0.66 pieces/meter (range = 0.05 to 1.34 pieces/meter) while debris volumes averaged 0.050 m^3/m^2 (range = 0.004 to 0.107 $m^3/m^{2)}$.

In-stream large woody debris diameters averaged 28 centimeters (range = 21 to 37 centimeters). Pre-harvest debris was significantly larger than post-harvest debris when comparing mean

TABLE 2. Comparison of mean diameter at breast height (cm) and Standard Deviation (SD) of standing and windthrown trees and mean diameter (cm) of in-channel large woody debris deposited pre- and post-harvest in 40 forest buffers associated with non-fish-bearing streams in northwest Washington.

	Standing Trees		Windthrown Trees		P-value[1]
Species	Diam.	SD	Diam.	SD	
Bigleaf maple	32.5	(8.6)	32.3	(3.6)	0.450
Douglas-fir	38.9	(11.4)	42.2	(7.4)	<0.001
Red alder	33.0	(12.2)	34.8	(8.1)	<0.001
Western redcedar	29.2	(13.5)	30.7	(7.9)	0.003
Pacific silver fir	28.4	(4.6)	33.8	(4.6)	<0.001
Western hemlock	30.2	(13.7)	30.0	(11.2)	0.114
	Pre-harvest		Post-harvest		P-value[1]
Large woody debris	30.0	(20.8)	24.9	(13.7)	<0.001

[1]P-values for mean tree diameters were based on Mann-Whitney rank sum tests and P-values for large woody debris diameters were based on a Student's t-test.

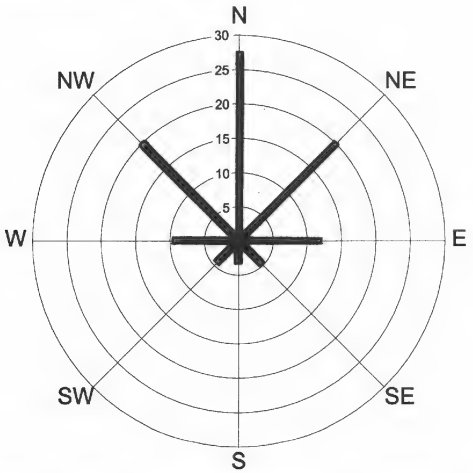


Figure 2. Percent of windthrown (uprooted and broken) trees falling in a given direction. Data is from 40 forest buffers in northwest Washington (n = 2,288).

piece diameters ($p<0.01$, Table 2). Pre-harvest debris averaged 30 centimeters in diameter while debris of post-harvest origin averaged 25 centimeters in diameter. Forty percent of pre-harvest debris pieces were larger than 30 centimeters in diameter while only 28 percent of post-harvest pieces fell into this category. Seven percent of pre-harvest debris and less than 2 percent of post-harvest debris was larger than 60 centimeters in diameter.

Approximately 66 percent of all large woody debris pieces were located within the bankfull streamflow zone; channel roughness was the primary function associated with 55 percent of these pieces while 32 percent stored sediment. Thirty-four percent of all woody debris pieces were suspended above the bankfull streamflow zone. While these pieces currently exert no direct influence on fluvial processes, they may become incorporated into the channel at a later date.

Figure 3 illustrates the function class distribution for both pre- and post-harvest large woody debris pieces. Eighty-five percent of pre-harvest debris pieces were located within the bankfull flow zone while 15 percent bridged the channel (Figure 3a). Twenty-eight percent of large woody debris pieces that entered streams post-harvest had a direct influence on channel processes (Figure 3b). Most post-harvest woody debris pieces bridged the stream channel (73 percent); post-harvest pieces accounted for 72 percent of all large woody debris pieces in this function class (984 of 1,364 pieces).

Sediment Storage

An average of 3.8 sediment wedges/100 meters of stream channel was recorded across the 40 sites. Seven sites had no wedge-associated storage within the study reach while 25 sites had between 0.5 and 25 m^3 of sediment stored in wedges (Figure 4). Average wedge volume was less than 3.0 m^3 for 28 of the 33 sites where wedges were present.

Large woody debris dams were the primary forming mechanism for 93 percent of all sediment wedges; the remainder were formed by bedrock or boulder obstructions. Debris dams comprised primarily of pre-harvest large woody debris formed 76 percent of inventoried wedges while post-harvest debris dams formed 5 percent of

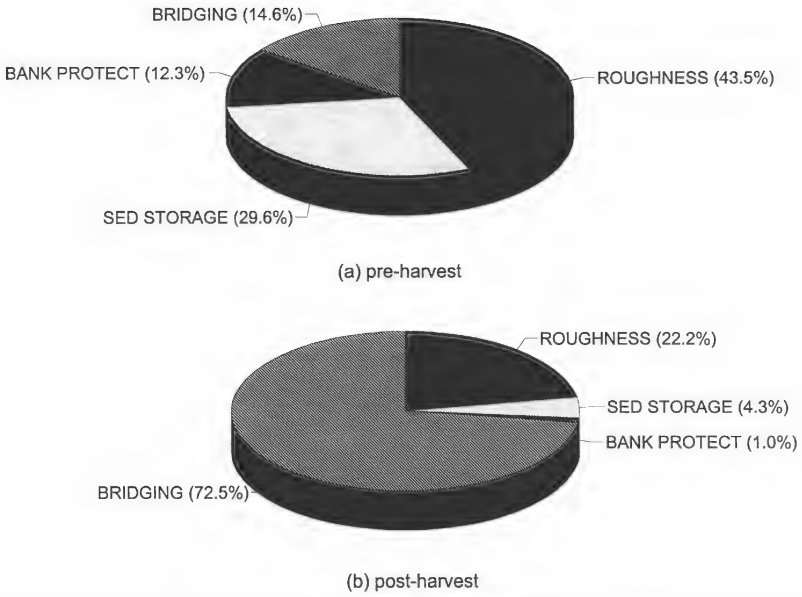


Figure 3. Function class distribution for in-stream (a) pre-harvest large woody debris (n = 2,611) and (b) post-harvest large woody debris (n = 1,357) associated with 40 non-fish bearing streams in northwest Washington.

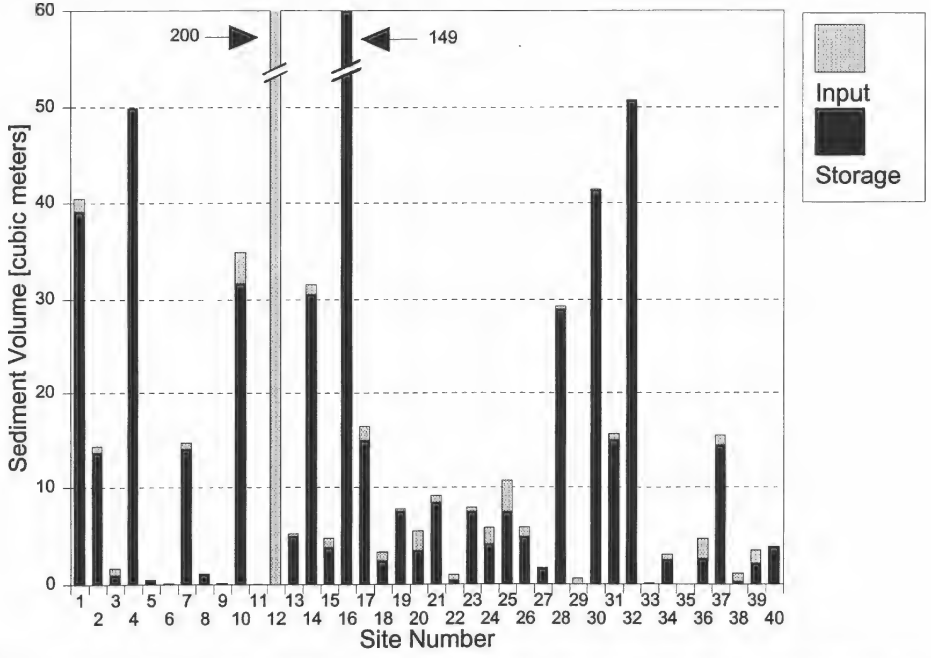


Figure 4. Sediment input and storage within 40 non-fish bearing streams in northwest Washington. Each bar represents one 150-meter stream reach. Sediment input is associated with uprooted buffer trees; sediment storage is associated with in-stream wedges created by obstructions or "dams".

wedges. Debris dams usually consisted of several pieces of woody debris anchored by larger key pieces of wood, boulders or bedrock. In many cases, the accumulated debris served to increase the height of the debris dam, thereby increasing its storage capacity. Debris smaller than our minimum piece size, and not included in the inventory, comprised a significant portion of some structures; debris dams composed wholly of such small debris also stored significant sediment volumes.

Sediment Delivery

Seventeen percent of uprooted trees delivered at least some sediment to stream channels. No sediment delivery occurred at three sites, <1 m^3 was delivered at 27 sites, between 1 and 2 m^3 was delivered at 8 sites, and >2 m^3 was delivered at two sites (Figure 4). A disproportionate amount of the total sediment volume delivered at all sites resulted from uprooting at a single site. A mass wasting event, probably triggered by uprooting of several large trees, delivered an estimated 200 m^3 of material to the channel (Figure 4). This site was characterized by steep channel-adjacent slopes comprised of deep, unconsolidated glacial outwash materials. This was the only site with this combination of geology and landform. Excluding sediment delivery at this site, inputs attributable to uprooted trees averaged 0.48 m^3 per 100 meters of stream channel.

Most windthrow-related sediment delivery to streams was associated with trees located within 3 meters of the channel edge. Eighty-five percent of the sediment delivered to stream channels at 39 of the 40 sites originated from within that zone (the mass wasting site was not included as its delivered volume exceeded the total of all other sites). Uprooted trees that fell toward or across the stream usually did not deliver sediment because the exposed portion of the rootwad faced away from the stream. Sediment inputs originating beyond 3 meters usually reached the channel as a result of trees sliding or rolling down a steep slope. However, in most cases, the rootwads of buffer trees did not move downslope after being uprooted.

At 23 of the 40 sites, sediment stored in wedges was approximately 10 times greater than the volume delivered to stream channels as a result of uprooting (Figure 4). Where delivery equaled or exceeded storage, channel gradients and/or valley confinement were generally not conducive to the formation of sediment wedges. High-gradient channels dominated by bedrock often had little capacity for sediment retention. Low gradient, unconfined channels contained large volumes of stored sediment, but most sediment was not stored in distinct wedges that met our inventory criteria. Sediment storage in these cases often occurred on adjacent floodplain landforms.

Discussion

Windthrow

In general, we found higher levels of windthrow than has been reported elsewhere in the Pacific Northwest (Table 3). Only one study, Steinblums (1978), reported average windthrow levels similar to those found by this study. The relatively high levels of windthrow found may result from

TABLE 3. Summary of reported buffer strip windthrow values in the Pacific Northwest.

Study	Location	# Sites	Buffer Age (years)	Windthrow[1] Range(%)	Mean(%)
This study	northwest WA	40	1-3	2-92[2]	33[2,3]
Mobbs and Jones (1995)	southwest WA	90	1	0-100[2]	5[2]
TFW (1994)	Washington	91	3-4	0-80[2]	10[2]
Sherwood (1993)	western OR	16	15-29	0-65[3,4]	12[3,4]
Andrus and Froehlich (1988)	western OR	30	1-6	0-72[3]	22[3]
Hobbs and Halbach (1981)	western WA	37	2-5	0-17[2]	5[2]
Steinblums (1978)	western OR	40	1-15	0-78[3]	29[3]

[1]In some cases, windthrow includes both uprooted and broken trees, while in others, only uprooted trees are included.
[2]expressed as a percent of stand stem density (trees/ha).
[3]expressed as a percent of stand basal area (m^2/ha).
[4]represents windthrow that occurred over the period 1977-1990; uses Steinblums (1978) reported post-windthrow volumes as a basis for estimated windthrow.

soil, topographic, and stand characteristics unique to the North Cascades region.

Relatively recent glaciation in the North Cascades (10,000 years before present) has shaped large-scale landforms and influenced soil characteristics in ways that may influence windthrow. The typically broad, glaciated valleys and hillslopes often offer little topographic protection from winds. Buffers on small streams are commonly associated with narrowly incised channels that drain broad, exposed hillslopes. Other regions of the Pacific Northwest with highly dissected drainages may be less susceptible to windthrow due to greater protection afforded by local topography. Furthermore, soils in the region are generally shallow (< 1 meter) and underlain by compacted glacial till or bedrock which restricts root penetration and anchoring. A perched water table typically persists throughout the wet season where drainage is impeded. Sites with shallow, wet soils are typically more subject to windthrow (Stathers et al., 1994).

The tree species composition of buffers may also influence windthrow occurrence. Pacific silver fir and western hemlock comprised over a third of all trees tallied at the 40 sites and were most susceptible to windthrow. Studies which reported relatively low levels of windthrow examined sites generally dominated by deciduous tree species such as red alder (Mobbs and Jones 1995; Timber, Fish and Wildlife 1994; Hobbs and Halbach 1981), which tend to be more windfirm than most species.

Site conditions documented in this study illustrate the influence of prevailing southerly winds on tree fall direction. Such information may suggest that buffer orientation could influence the degree of windthrow at a given site. That is, one might expect buffers oriented perpendicular to the direction of prevailing winds would experience higher levels of windthrow than those oriented parallel to prevailing wind direction. In this study, we documented a wide range of windthrow levels and tree fall directions. However, we found no evidence to indicate that buffer orientation influenced windthrow levels. It is likely that the level of windthrow occurrence at a given site is a complex interaction of a range of factors which vary in their degree of influence from site to site.

In-Channel Large Woody Debris

Buffer windthrow increased the number of in-channel large woody debris pieces by 34 percent across the 40 sites within one to three years after harvest. Such short-term increases in wood loading suggests that buffer windthrow is a significant mechanism by which debris is recruited to streams soon after harvest. Furthermore, tree fall patterns we documented suggest that woody debris recruitment from forest buffers is non-random, with trees tending to fall towards the north. For streams with east-west orientations, this suggests that much of the debris recruitment occurring within a few years post-harvest will originate from the south side of the stream.

Much post-harvest debris recruited to channels was suspended over the stream and will do little to influence channel processes in the near-term. These pieces must undergo a secondary recruitment phase where they break apart and enter the bankfull flow zone. The time between the initial windthrow and this secondary phase will vary depending on the species, size, and condition of wood pieces. Secondary recruitment of smaller hardwoods is likely to occur in a matter of a few years while larger conifers may remain suspended for decades.

The role of woody debris in retaining sediment in small headwater stream channels of the northwest has been documented previously (O'Connor and Harr 1994; Potts and Anderson 1990; Megahan 1982). Potts and Anderson (1990) found that organic matter accounted for over 60 percent of total sediment storage within eight reaches of first to third order channels in western Montana. Similarly, Megahan (1982) reported that organic material formed 76 percent of channel obstructions associated with sediment storage in seven small drainages in the Idaho batholith. Removal of this material via salvage logging or stream cleanout would likely destabilize the channel (Bilby 1984) and increase sediment export from the system (O'Connor and Harr 1994). Thus, buffers may provide a long-term source of large woody debris which helps create and maintain debris loads and reduce sediment yields. However, large woody debris recruited as a result of windthrow (post-harvest debris) was significantly smaller in diameter than debris recruited prior to buffer establishment (pre-harvest debris). A portion of the pre-harvest debris load consisted of larger pieces recruited from the original forest. Smaller debris generally has a shorter residence time and may be less effective at creating and maintaining sediment storage sites compared to larger pieces.

Sediment Delivery

In most cases, the volume of sediment delivered to stream channels as a result of post-harvest windthrow was relatively small. Sediment delivery at all sites averaged 1.43 m^3/uprooted tree. However, the average was only 0.16 m^3/uprooted tree at 39 of the 40 sites where mass wasting was not associated with uprooted trees. Except under the unusual physical conditions present at this single site, windthrow did not accelerate mass wasting. Andrus and Froehlich (1988) reported an average delivery of 0.87 m^3/uprooted tree for windthrow in the Oregon Coast Range. They concluded that the volume of sediment delivered to streams was usually small compared to overall watershed sediment yield and that uprooted trees did not accelerate mass wasting. Increases in sediment inputs attributable to windthrow may be offset by sediment storage sites created by recruited woody debris; however, we found that relatively few post-harvest debris pieces were currently storing sediment (Figure 3b).

Most windthrow-generated sediment delivery originated from trees rooted in the streambank. This zone generally extends outward 3 meters from the channel edge and accounted for approximately 85 percent of windthrow-generated sediment delivery. While harvest of trees in this zone might reduce sediment input to streams, other buffer functions such as rooting strength, woody debris recruitment, and shade would be reduced or eliminated.

Conclusions

The magnitude of windthrow in buffers bordering small, non-fish bearing streams in northwest Washington is highly variable. Even so, observed windthrow levels were generally higher than those reported in studies for other areas in the Pacific Northwest.

In a managed forest landscape, buffer windthrow is likely the most significant mechanism by which large woody debris is recruited to stream channels. Such debris is an important structural component in small headwater streams where it forms debris jams which trap and store sediment. However, for narrow, confined stream channels, windthrown trees are commonly suspended above the channel, providing little immediate influence on channel processes and sediment routing.

Generally, results of this study indicate windthrow is not a significant source of sediment delivery to stream channels. In addition, volumes of sediment delivered to streams as a result of windthrow were small relative to the amount stored within the channel. A notable exception occurred at a single site where uprooted trees accelerated mass wasting and delivered large volumes of sediment to the channel. This was the only site where the forest buffer developed in deep, unconsolidated glacial outwash materials.

Forest buffers are often established to maintain a range of ecosystem functions; windthrow may compromise some of these functions (e.g., shade, water quality, streambank stability) while at the same time enhancing others (e.g., large woody debris recruitment, sediment storage). The extent to which these functions are affected will depend on the magnitude and spatial and temporal occurrence of windthrow.

Acknowledgements

Doug Couvelier and Adrian Garcia worked under difficult terrain and weather conditions to collect field data for this project. The Washington Department of Natural Resources - Northwest Region provided most of the financial support. Additional funding was provided by the Washington Department of Ecology. Crown-Pacific Corporation, The Campbell Group, Trillium Corporation, and the Department of Natural Resources assisted in identifying potential study sites and provided access. In addition, C. Andrus, R. Beschta, R. Bilby, W. Megahan, K. Sullivan, J. Agee, R. Feller, and three anonymous reviewers provided useful comments and suggestions on earlier versions of the manuscript.

Literature Cited

Andrus, C. W. and H. A. Froehlich. 1988. Wind damage within streamside buffers and its effect on accelerated stream sedimentation in coastal Oregon streams. Unpublished Manuscript. Department of Forest Engineering. Oregon State University, Corvallis, Oregon.

Bilby, R. E. 1984. Removal of woody debris may affect stream channel stability. Journal of Forestry. 82:609-613.

Bisson, P. A., R. E. Bilby, M. D. Bryant, C. A. Dolloff, G. B. Grette, R. A. House, M. L. Murphy, K. V. Koski, and J. R. Sedell. 1987. Large woody debris in forested streams in the Pacific Northwest: past, present and future. *In* T. Cundy and E. Salo, eds. Proceedings of a symposium: Streamside Management—Forestry and Fisheries Interactions. Feb 12-14, 1986. Inst. of For. Res., Univ. of Washington, Seattle, Washington. pp. 143-190.

Gratkowski, H. J. 1956. Windthrow around staggered settings in old-growth Douglas-fir. Forest Science 2:60-74. Hobbs, D. and T. M. Halbach. 1981. Streamside management zone inventory. Washington Department Ecology, Water Quality Planning. DOE 81-12. Olympia, Washington.

Megahan, W. F. 1982. Channel sediment storage behind obstructions in forested drainage basins draining the granitic bedrock of the Idaho batholith. *In* F. J. Swanson, ed. Sediment Budgets and Routing in Forested Drainage Basins. USFS Gen. Tech. Rpt. PNW 141. pp. 114-121.

Mobbs, M. W. and B. C. Jones. 1995. Quinault Indian Nation -Riparian management zone project report. Quinault Indian Nation, Taholah, Washington. 50 p.

Montgomery D. R. and J. M. Buffington. 1993. Channel classification, prediction of channel response, and assessment of channel condition. Wash. Dept. Nat. Res. Report TFW-SH10-93-002, Olympia, Washington. 86 p.

Moore, M. K. 1977. Factors contributing to blowdown in streamside leave strips on Vancouver Island. Land Management Report No. 3. British Columbia Ministry of Forests, Victoria, British Columbia, Canada.

Naiman, R. J., T. J. Beechie, L. E. Benda, D. R. Berg, P. A. Bisson, L. H. MacDonald, M. D. O'Connor, P. L. Olson, and E. A. Steel. 1992. Fundamental elements of ecologically healthy watersheds in the Pacific Northwest coastal ecoregion. *In* R. J. Naiman, ed. Proceedings of a symposium: Watershed Management: Balancing Sustainability and Environmental Change. November 27-29, 1990. Center for Streamside Studies. University of Washington, Seattle, Washington. pp. 127-188.

O'Connor, M. D. and R. D. Harr. 1994. Bedload transport and large organic debris in steep mountain streams in forested watersheds on the Olympic Peninsula, Washington. Washington State Department of Natural Resources, Timber/Fish/Wildlife Program. TFW-SH7-94-001. Olympia, Washington. 125 p.

Potts, D. F. and B. K. M. Anderson. 1990. Organic debris and the management of small stream channels. Western Journal of Applied Forestry. 5(1):25-28.

Rollerson, T. 1982. Relationships between windthrow and various environmental variables. *In* Land Management Report No. 10: Soils Interpretations for Forestry. Province of British Columbia: Ministry of Environment, Ministry of Forests. Victoria, British Columbia, Canada. pp. 41-62.

Ruth, R. H. and R. A. Yoder. 1953. Reducing wind damage in the forests of the Oregon Coast Range. U.S.D.A. Forest Service, Pacific Northwest Forest and Range Experiment Station. Research Paper No. 7. 30 p.

Sherwood, K. 1993. Buffer strip dynamics in western Oregon Cascades. M.S. Thesis. Forest Engineering Department, Oregon State University, Corvallis, Oregon.

Stathers, R. J., T. P. Rollerson, and S. J. Mitchell. 1994. Windthrow handbook for British Columbia forests. B.C. Min. For., Victoria, British Columbia. Working Paper 9401. 31 p.

Steinblums, I. H. 1978. Streamside buffer strips: survival, effectiveness, and design. M.S. Thesis. Forest Engineering Department, Oregon State University, Corvallis, OR.

Steinblums, I. H., H. A. Froehlich and J. Lyons. 1984. Designing stable buffers for stream protection. Journal of Forestry. 82(1):49-52.

Steinbrenner, E. C. and S. P. Gessel. 1956. Windthrow along cutlines in relation to physiography on the McDonald Tree Farm. Forestry Research Note No. 15. Weyerhaeuser Timber Company, Tacoma, Washington. 19 p.

Sullivan, K., T. Lisle, C. A. Dolloff, G. E. Grant, and L. M. Reid. 1987. Stream channels: the link between forests and fishes. *In* T. Cundy, and E. Salo, eds. Proceedings of a symposium: Streamside Management - Forestry and Fisheries Interactions. February 12-14, 1986. Institute of Forest Resources, University of Washington, Seattle, Washington. pp. 39-97.

Timber, Fish and Wildlife Field Implementation Committee. 1994. Washington 1993 riparian management zone survey. Washington State Department of Natural Resources, Timber/Fish/Wildlife Agreement, TFW-000-94-001. Olympia, Washington. 58 p.

Received 31 October 1997
Accepted for publication 26 August 1998

Northwest Science Forum

Northwest Science Forum provides an opportunity to articulate and discuss scientific issues in a less structured format than peer-reviewed articles. The Forum publishes short articles, opinion pieces, and letters with a focus on science and natural resource issues in the Pacific Northwest. Although the Forum is not peer-reviewed, it is edited for format and clarity. Articles should generally be less than 2000 words and contain minimal literature citations. Letters in response to articles are particularly encouraged; the original author will normally be given a chance to respond to the letter as well. There are no page charges or reprints associated with the Forum, and participants need not be members of the Northwest Scientific Association. Please send all submissions, including two hard copies and an electronic copy (any recent version of Word or WordPerfect for DOS), to the Editor.

Clare M. Ryan, College of Forest Resources, University of Washington, Box 352100, Seattle, Washington 98195-2100

Challenges and Opportunities in Collaborative Natural Resource Management

Collaboration, community dialogue, partnerships, cooperation, participation, and consensus. Each of these words reflects aspects of a current trend towards more local and regionally based decisions in natural resource management. Local planning groups such as the Quincy Library Group in California, the Applegate Partnership in Oregon, and Henry's Fork Watershed Council in Idaho are, in spite of their problems and controversies, familiar components of the natural resource management landscape, and often held up as models for future land management (Brick, 1998).

For well over a decade, federal, state and local officials have been encouraged to embrace and use collaborative approaches to decision making. Recently, the Clinton Administration's *National Performance Review* presented a number of recommendations intended to improve government in general, and the process of federal rulemaking in particular. The "reinventing government" report urged federal agencies to expand the use of alternative dispute resolution techniques, and in particular, make greater use of regulatory negotiation (National Performance Review, 1993). A follow-up report, *Common Sense Government* (Gore, 1995), highlights additional successful reinvention efforts throughout the federal government, many of which involve alternative dispute resolution and negotiation processes. In addition, state legislation promotes negotiation and collaboration in siting disputes and land use planning (Bingham and Miller, 1987; Rabe, 1994).

In attempting to respond to this encouragement, several federal resource management agencies and many states have begun to institutionalize collaborative resource management and planning efforts. For example, the U.S. Bureau of Land Management set up Resource Advisory Councils (RACs) in 1995. These are locally based, collaborative groups that provide advice to BLM on a variety of issues affecting the management of public lands. The Forest Service uses collaborative planning and consultation in developing many of its National Forest Management Plans. Further, in his Fiscal Year 1996 Report, Chief Michael Dombeck of the U.S. Forest Service cited "collaborative stewardship" and "partnerships" a number of times as guiding principles for the how the Forest Service will conduct their work in the future. Finally, the U.S. Fish and Wildlife Service

has used consensus processes to deal with endangered species and development conflicts.

Agency participants at all levels of government have been struggling to define what this new trend implies for them, as they attempt to shift towards a more collaborative style of decision making. A broader question asks what this trend towards consensus building and collaborative management means for the role of agencies, policymakers and decision-makers in natural resource management.

Why Collaborate?

In the last decade or so, resource managers have experienced a significant increase in and proliferation of the number and types of interest groups, or stakeholders, demanding to be heard and incorporated into the policy making process. It is hoped that by working collaboratively with stakeholders before decisions are made or policies are adopted, more complete information will inform the policy maker (Ozawa, 1991; Yaffee and Wondolleck, 1995). In addition, mutual understanding of the issues at stake will be fostered, as will communication and trust between the parties involved (Carpenter and Kennedy, 1988; Wondolleck, 1988). Hence, acceptable decisions will result rather than decisions that are contested in lengthy judicial or administrative appeals processes (Bingham, 1986; Susskind and Cruikshank, 1987).

As two analysts correctly stated, "land managers...are at their wits' end in trying to placate all of them...and are part of not one, but several, triangles of interests. Perhaps a new term for this changed situation would be 'tangles' of interests. Each knot in the tangle would represent what is now called a stakeholder" (Clarke and McCool, 1996). The responsibility, wanted or not, of untangling the many interests in order to make management decisions has fallen to resource management agencies and managers. Responding to this new reality requires those managers to play a variety of new roles if they hope to be successful in untangling the interests and needs of multiple stakeholders in order to make required resource management decisions that can be successfully implemented.

Balancing New Roles in Collaborative Processes

One recent study presents a new conceptualization of agency roles in collaborative processes, drawing from the experiences of natural resource managers and environmental regulators at the federal level (Wondolleck and Ryan, 1997). If they were to be effective, each of the collaborative processes required that the agency participants adopt new and different roles. The experiences of agency participants in these different settings suggest a new conceptualization of agency behavior—one that merges the distinct yet essential roles of *leader*, *partner* and *stakeholder*. Furthermore, and contrary to conventional wisdom, if agencies acted as only a facilitator of the process, this was found to be ineffective and inappropriate in most cases.

Being a Leader

The leadership of the agency participant is fundamentally different and more central to the process because of their unique and distinct decision making authority. The agency provides an opportunity for collaboration to take place, and their presence and authority gives the collaborative process legitimacy. Additionally, because the collaborative approach tends to be a new one for *all* parties involved, the agency participant is the one that is most often looked to for guidance and leadership. In the context of the study, leadership was provided or clearly needed, in three realms: leadership of the collaborative process itself, leadership about the issues under discussion, and leadership about the decisions to be made.

Being a Partner

The cooperative, problem-solving dimension of a collaborative process provides the focus for parties to engage as partners in the effort. Partnership implies sharing a problem, opportunity or interest in common with other individuals or groups, and being willing to work together in order to solve a shared problem or pursue a common vision. Being a partner is a uniquely challenging role for agency participants, as it is the role that is least consistent with traditional agency procedures. As a result, numerous barriers were posed by the perceptions, stereotypes, and expectations of participants both from within the agency

as well as from other participant groups. At times, being an effective partner requires strong leadership, and this tension between leadership and partnership is a challenge experienced by many agency participants in collaborative processes.

Being a Stakeholder

Effective stakeholder behavior is a cornerstone to successful collaborative processes. Stakeholders should be clear about their interests, know how their interests are similar or different from those of other stakeholders, understand their priorities within these interests, and where tradeoffs might acceptably be made. Agency participants must be aware of what interests and responsibilities are unique to them, and ensure that they advocate for and accommodate those interests in any agreements that are reached. Perhaps the greatest failing of agency participants in this study was their lack of preparation and action in recognition of this stakeholder role.

What little attention has been given in the literature to the specific question of agency role has most often focused on facilitation (Carpenter and Kennedy, 1988). Some have argued that agencies should serve as the "facilitator of a community of interests" when working in collaborative settings (Sirmon et al., 1993). This characterization is both limiting and misleading, making agency officials less effective than they might be. Many collaborative processes do indeed need a facilitator to assist the parties in effective communication, negotiation and problem solving. But the facilitator should not be the same official who is responsible for representing the agency's interests at the table. Combined agency facilitation and representation proved to be not only ineffective, but also oftentimes counterproductive to the consensus-seeking objective of the process (Wondolleck and Ryan, 1997).

The tasks of being a leader, stakeholder and ultimately a partner imply an array of different skills, roles, and interactions with other participants in collaborative processes. These new skills and behaviors have implications for agencies and other decision-makers that attempt to undertake such efforts. It is apparent that at one level the contemporary resource management agency's role is far richer, more complex, and more difficult to fulfill than has been described in the theoretical literature. Agencies must at the same time fulfill the multiple roles of expert, stakeholder, and decision-maker, and, most importantly, be an effective leader and partner in the decision making process. Unfortunately, there is no formula dictating when each role should be performed, or how to successfully play multiple roles simultaneously, which is what is required in collaborative resource management processes.

Collaborative Resource Management Challenges and Opportunities

Some critics charge that collaborative processes may totally disempower those citizens not represented by organized interests, and that only the "lowest common denominator ideas survive the process" (McCloskey, 1996). Others claim that collaboration on many resource issues is unlikely to succeed because the interests and needs of the stakeholders are so different that the chance of agreement is nearly zero. Still others are alarmed over the implications of including citizen participation on a par with bureaucratic experts, and the dissolution of hierarchical authority relationships in favor of shared power with nongovernmental stakeholders (Moe, 1994).

Despite these criticisms, the reality is that resource managers are now being called upon to "untangle" the many interests that want to participate in resource management decisions. Emerging issues in Pacific Northwest, particularly the impending listing of the chinook salmon (*Oncorhynchus tshawytscha*) as a threatened species, and the projected growth in population and related pressures on natural resources, are forcing managers to deal with these issues immediately. Policy makers and managers are *not* waiting on scholars to decide whether such collaborative arrangements are appropriate or not. They are choosing and using alternative institutional arrangements that defy traditional approaches to bureaucracy (Weber, 1998), and, admittedly, may be stumbling as they navigate along the way.

However, given the alternatives of policy gridlock and litigation, collaborative resource management does offer a needed forum and opportunity to begin to address multiple interests and make pressing management decisions. Resource managers will need to develop a variety of skills to help them successfully manage and participate in collaborative processes. Integral to their "untangler" role is a need to play critical

leadership, partnership, and stakeholder roles. In addition, skills and techniques are needed to help managers identify and measure what the key interests are and how to effectively incorporate those interests into the policy making process.

Further thought is needed regarding *what types* of decisions are appropriate for collaborative processes. It is clear that every decision cannot be made via a collaborative process. In fact, many managers are bumping up against institutional limits in terms of how many processes can be initiated and managed, in addition to limits on the participation by key stakeholder groups. Finally, mechanisms to foster interagency cooperation and collaboration in such ventures are sorely lacking. Alternative institutional arrangements that foster collaborative management must be investigated and developed.

Literature Cited

Bingham, G.A.1986. Resolving Environmental Disputes: A Decade of Experience. The Conservation Foundation, Washington, D.C.

Bingham, G.A. and D.S. Miller. 1987. Prospects for resolving hazardous waste siting disputes through negotiations. Natural Resource Lawyer 18:473-489.

Brick, P.D. 1998. Collaboration and legitimacy: finding a political niche for collaborative conservation. Paper presented to the American Society for Public Administration National Conference, May 1998.

Carpenter, S.L. and W.J.D. Kennedy. 1988. Managing Public Disputes: A Practical Guide to Handling Conflict and Reaching Agreements. Jossey-Bass, San Francisco.

Clarke, J.N. and D.C. McCool. 1996. Staking Out the Terrain: Power and Performance Among Natural Resource Agencies. State University of New York Press, Albany.

Gore, A. 1995. Common Sense Government: Works Better and Costs Less. Random House, New York.

Gray, B. 1989. Collaborating: Finding Common Ground for Multiparty Problems. Jossey-Bass, San Francisco.

Heclo, H. 1978. Issue networks and the executive establishment. In A. King, ed., The New American Political System. Washington, DC: American Enterprise Institute.

McCloskey, M. 1996. The skeptic: collaboration has its limits. High Country News 28 (May 13, 1996).

McCool, D. 1990. Subgovernments as determinants of political viability. *Political Science Quarterly* 105 (Summer).

Moe, R. 1994. The reinventing exercise: misinterpreting the problem, Misjudging the Consequences. Public Administration Review 54 (March-April).

National Performance Review. 1993. Creating a Government that Works Better and Costs Less. Report of the National Performance Review. Government Printing Office, Washington, D.C.

Ozawa, C.P. 1991. Recasting Science: Consensual Procedures in Public Policy Making. Westview Press, Boulder, CO.

Rabe, B.G. 1994. Beyond NIMBY: Hazardous Waste Siting in Canada and the United States. Brookings Institution, Washington, D.C.

Sirmon, J., W.E. Shands, and C. Liggett. 1993. Communities of Interests and Open Decision-Making. Pinchot Institute for Conservation, Washington, D.C.

Susskind, L. and J. Cruikshank. 1987. Breaking the Impasse: Consensual Approaches to Resolving Public Disputes. Basic Books, New York.

Weber, E.P. 1998. Pluralism by the Rules: Conflict and Cooperation in Environmental Regulation. Georgetown University Press, Washington, D.C.

Wondolleck, J.M. 1988. Public Lands Conflict and Resolution: Managing National Forest Disputes. Plenum Publishers, New York.

Wondolleck, J.M. and C.M. Ryan. 1997. What hat do I wear now? Agency roles in collaborative processes. Manuscript submitted for publication.

Yaffee, S.L. and J.M. Wondolleck. 1995. Building knowledge pools and relationsheds. Journal of Forestry 92(5):68.

Book Reviews

Land Mammals of Oregon

B.J. Verts and Leslie N. Carraway, 1998, University of CaliforniaPress, Berkeley, California ($80.00)

The long-awaited Land Mammals of Oregon is now available and will not be a disappointment to those who have been anticipating its arrival. This book is the most complete and up-to-date reference that exists for Oregon's land mammals. The book is much more comprehensive and detailed than the typical "Mammals of (state)" book and is a required reference for every mammalogist, wildlife biologist, and naturalist interested in mammals of the northwest. The authors have examined over 55,000 museum specimens and provide accounts of morphology, distribution, life history, ecology, and behavior of the 136 species of mammals in Oregon. The book is a lengthy 668 pages and contains 122 color photographs, 36 black and white photographs, 140 maps, and 150 line figures. A state map with counties, major cities, and landmarks is provided for quick reference locations.

The book is much more than a description of Oregon mammals. In the first chapter, Verts and Carraway review the basic biology of mammals by including a list, description, and definitions of mammalian characteristics, illustrations of skull and skeletal features, and a concise summary on the science of naming mammals. This introduction is followed by a brief history of mammalogy in Oregon with short biographies and discussions of collecting trips, early discoveries, and contributions of notables such as Spencer Baird, C. Hart Merriam, Vernon Bailey, Alex Walker, and many others.

Chapter 3 is a concise easily accessible checklist of common and scientific names of the 136 species from 27 families and seven orders of mammals represented in Oregon. The authors then describe the geological history that helped shape the prehistoric and recent mammalian faunas of Oregon. Illustrations and descriptions are included for some of the more "bizarre" and now extinct mammalian forms from the Tertiary through the Quaternary periods. Verts and Carraway then describe the nine physiognomic provinces in Oregon that have influenced the biogeographical affinities of present-day mammals. In an eye-opening chapter on Zoonoses, Verts and Carraway remind mammalogists of the potential danger to various viral, bacterial and rickettsial diseases that can be contracted while handling mammals.

The heart of the book can be found in chapters 7-13, one for each of the seven orders of mammals represented in Oregon. Each chapter starts with a section describing the characteristics and a brief history of the order and its relevance to Oregon. This introduction is followed by a very readable and understandable key to the families and species of that order. Key characters include skull, teeth, and skeletal features, as well as easily distinguishable external morphological and pelage characteristics. The real strength of this book is in the detail provided on the biology of each species. Major topics covered include the history of scientific naming of the species, description and distinguishing features of the skull, skeletal, teeth and external features, and the species distribution in Oregon and throughout its geographic range. Site locations for collecting points are clearly marked on a map of Oregon and a general range map is included for the species distribution throughout North America. A section on Geographic Variation including subspecies or geographic races shows the diversity within the species across its zoogeographical range. The sections on Habitat and Density, Diet, Reproduction, Ontogeny, and Mortality, Habitats, and Remarks provide detail for even the most seasoned mammalogist. These sections include information on food habits and foraging behavior, habitat preferences, denning and nesting behavior, population dynamics, survival and mortality rates, breeding season, litter sizes, mating systems, growth and development, sociality, daily and seasonal activity, and general ecological relationships to habitat and other species. Diagnostic and expertly drawn skulls (by Leslie Carraway) are illustrated for each species. A

helpful table that includes the measurements of skull and skin characters for females and males separated for different regions of Oregon is provided for all species for which adequate data were available. For species in which life history data are not available for Oregon populations, reference often is made to comparable data from other areas of North America. Although the authors rely heavily on published literature (2,925 references are cited), much of the data are from their own research, collections, and personal experiences of working with Oregon's mammals. A comprehensive glossary is included and the index provides easy reference to specific items in the text. I appreciated the authors' candor in their interpretation of much of the literature when they caution the reader about the authenticity of some records or question the conclusions from some published literature (including a reference of my own!).

I could not help but appreciate the personal touch provided in the Remarks section of each species account. Verts and Carraway use this section to express their personal feelings about wildlife management, conservation measures, mammal taxonomy, predator control, endangered species, responsibility of landowners and industry, and dispelling current myths. For instance, "...unholy taxonomic mess..." (referring to grizzly bears); ".....saga of the fur seal appears as alternating periods of wantonness and remorseful conservatism combined with questionable management"; "....we are strongly skeptical of the proclaimed historic occurrence of the species [mountain goat] in the state"; or with respect to making "pets" of wild mammals, "...we strongly advocate leaving wild mammals in the wild!"; or "....don't waste good tomato juice [to remove skunk odor] add a little vodka and drink it; it won't reduce the odor, but the odor won't bother you so much!".

Land Mammals of Oregon should be a blueprint by which all future State species- accounts books are formatted. The book is nicely designed and printed in high quality, the information is thorough and up-to-date (including references from 1997), and the content is unsurpassed. The editorial style is professional and easy to read. The only negative aspect of the book is the color of the cover which is an Oregon Duck yellow and green. This is blasphemous to an Oregon State Beaver. The University of California Press apparently has a satirical sense of humor.

—Jerry O. Wolff (former Oregon State Beaver)
Department of Biology
Campus Box 526080
The University of Memphis
Memphis, TN 38152-6080
jwolff@memphis.edu

American Pronghorn: Social Adaptations and the Ghosts of Predators Past

John A. Byers, 1997, University of Chicago Press
(Price not stated on book)

"Those who do not consult the past are condemned to be fooled by the present." With this statement, John Byers sums up his excellent book on the social organization of pronghorns. Based on data collected over 14 years on the National Bison Range, Byers notes that much of the pronghorn's behavior is difficult to explain under current ecological conditions, but makes good sense when viewed in the light of recent evolutionary history. Anyone who has seen a pronghorn run will see some truth in Byers's assertion that they are "truly Olympian runners in a world of notably less-than-Olympian predators". Byers argues that the fleetness and gregariousness of pronghorns have little benefit to offset their costs under current conditions, but were probably advantageous until a horror show of North American predators went extinct at the end of the Pleistocene.

Byers presents a wide range of data that cohesively support his thesis. In the absence of predation on adult pronghorns, there are no demonstrable benefits to group-living. Predation on fawns by coyotes is still intense, but in this instance the pronghorn's first line of defense is concealment, so grouping yields no benefit. Data on feeding rates and social interactions suggest that grouping now has a net cost. (One can quibble here - the costs appear rather small to me). However, if the interactions of pronghorns and extinct predators like the Giant Short Faced Bear resembled those of modern carnivores and antelopes, it seems likely that grouping formerly reduced the risk of predation.

Detailed observations on a wide range of behaviors dovetail into this interpretation. Dominant females maintain a central position in herds, close to neighbors, as though shielding themselves from attack. Females engage in an elaborate and costly evaluation of males before mating, but do not prefer older, larger or parasite-free males. What do they seek? Good runners. In Byers's words:

> When females assay male vigor they in effect assay most of the male's functional genome... Throughout most of the evolutionary history of pronghorn, when stalking, coursing and sprinting predators pursued individuals, offspring of both sexes stood to gain from maternal selection of vigorous males. Sexual selection in pronghorn has therefore acted largely in concert with, rather than in opposition to, natural selection.

The book applies solid data to many prominent issues in behavioral ecology. For example, high ranking mothers give birth earlier than low ranking mothers. Early born female fawns (but not male fawns) attain higher juvenile rank, and this effect persists into adulthood. Given these findings, evolutionary theory predicts that dominant females should invest more in daughters than in sons. Following this expectation, dominant females give birth to significantly more daughters than sons (and invest more energy in the growth of daughters). Byers gives an interesting discussion of these findings relative to the Trivers-Willard hypothesis and alternative explanations.

A second interesting example is based on the finding that old females are more likely to raise their fawns than are young females. Byers notes this might be interpreted as support for the hypothesis that pronghorns trade current reproduction against residual reproductive value to maximize lifetime reproductive success, but the conclusion would probably be wrong. He found no evidence that reproductive effort varies with age. Instead, older females simply get better at concealing fawns and defending them from predation.

These are just a few examples from a broad range of topics that Byers has addressed. Those who are interested in behavioral development, social organization, sexual selection, social dominance, sex ratios, and reproductive energetics will find interesting data and interpretation in this book. I didn't agree with every conclusion, but found the great majority of the analyses to be thoughtful, interesting and convincing. Several general discussions of broad points made me stop and consider the basic assumptions I make in interpreting behavior (e.g. a discussion in Chapter six on the concept of social dominance in explanations of antagonistic interactions).

This book is far easier to read than a typical academic monograph, as illustrated by the following passage: "A cohesive wapiti harem is like an amoeba—pseudopodia may extend or retract, but there is an essential unit resilient to fragmentation. Pronghorn harems are more similar to a

handful of ball bearings on a table." I found I could read several chapters in a sitting, which is a strong testament that the writing is good.

All in all, this is an excellent addition to the traditionally excellent Chicago series on behavior and ecology.

—Scott Creel
Department of Biology
Montana State University
Bozeman Montana 59717

The Great Blue Heron

Robert W. Butler, 1997, University of British Columbia Press, Vancouver, B.C. ($39.95)

Recently, leading journals (e.g., Conservation biology) published editorials that criticized the current desk-biology approach in conservation biology. Still today, there is a substantial lack of natural history data for many species as evident in many multiple-species conservation plans. *The Great Blue Heron* by Robert Butler is an example that shows otherwise. In his book, Butler provides the reader with an extensive summary of the natural history of the great blue heron (*Ardea herodias*), and at the same time, Butler demonstrates superbly how an integrative approach can enhance our understanding of how natural selection influences the natural history of species. Similarly, Butler demonstrates that by including between species comparisons, the non-exciting approach of natural history summaries can be circumvented.

A central tenant of conservation biology is that environmental issues must be expressed to appeal to a variety of people that differ in background and interests. *The Great Blue Heron* is a good example of how this can be accomplished. Butler sets the stage in the introduction "the seashore sentinel" that briefly outlines the major components of the ecosystem the northwest coast great blue heron (*A. herodias fannini*) occupies. Following this are eight chapters that explore the natural history of the great blue heron, mainly focusing on the northwest coast great blue heron (great blue heron hereafter). The chapters are illustrated with 24 color plates, 30 black and white pictures, 17 figures and 18 tables. The book ends with an epilogue that discusses cultural values of the great blue heron in past and today's societies and four appendices: 1) Historical records of great blue heron colonies on the British Columbia coast; 2) Length-mass regression equations of fish caught in beach seines on Roberts Bank, Fraser River delta, BC; 3) Effects of increased disturbance on heron populations; and 4) List of common and scientific names used in text.

Chapter one introduces general aspects of the great blue heron's natural history (e.g., distribution, morphology). In this chapter the reader finds useful summaries about the distribution, population size and studies accomplished on the great blue heron with an emphasis on British Columbia. The major focus of chapter two is to introduce the Strait of Georgia and Puget Sound ecosystem to the reader. This chapter begins very broadly by discussing the flora and fauna of this ecosystem as well as historical and conservation issues. This is followed by an excellent description of the great blue heron's food web, mainly driven by the presence/absence of eelgrass (*Zostera marina and Z. japonica*). Butler ends this chapter by describing the field methodology and his study sites, Sidney Island and Fraser River delta. Aspects of foraging and diet of the great blue heron are described in chapter three. Here, Butler provides detailed summaries of the great blue heron's diet as well as the availability of prey items during the winter and breeding season, presented in four breeding stages. In this chapter readers will also find useful information on the foraging behavior and patterns of the great blue heron, including how these are influenced by "tidal windows". Chapter four is devoted to social and territorial behaviors of the great blue heron. Topics such as mate choice and arrival time at the colonies are discussed. In chapter five, Butler discusses the breeding ecology of the great blue heron, including information on the distribution of heron colonies in the Strait of Georgia, the influence of temperature and food availability on the onset of breeding, as well as on nest site selection, egg and clutch size, chick growth, siblicide, nesting success and post-fledgling care. In chapter six, seasonal habitat requirements of the great blue heron are presented. Chapter seven begins with a comparison of life history traits among heron species, focusing mainly on the great blue heron and the grey heron (*Ardea cinerea*), but also among great blue heron subspecies. The major focus in this chapter is on demographic variables such as survival of eggs, chicks, juveniles and adults but also on mortality factors and population growth and limitation. The book concludes by describing the threats to populations of the great blue heron. The survival of great blue heron populations in British Columbia is influenced by habitat destruction (both feeding as well as nesting habitat), human disturbance and pollution.

Overall, I highly recommend *The Great Blue Heron* to scientists that study great blue herons as well as to naturalists that would like to learn

more about this charismatic species. More importantly, I recommend this book as an example of how ecological concepts and conservation issues can be presented to a variety of readers. Books like this are an important contribution towards narrowing the prevailing communication gap between conservation biologists and the public.

—Matthias Leu
College of Forest Resources/
Wildlife Science Group
Box 352100
University of Washington
Seattle, WA 98195

Preserving Nature in the National Parks: A History

Richard W. Sellars, Yale University Press,
($35 cloth ,ISBN 0-300-06931-6)

Most people think that national parks are a good idea—for protecting wildlife, for enhancing biological diversity, for recreation. But opinions within the scientific community and the general public on how the United States National Park Service should manage its land holdings vary dramatically, and controversy has sharpened in the past decade as stakeholders and interest groups become more actively involved in the debate over the "appropriate" use of public lands.

As Richard Sellars tells us in *Preserving Nature in the National Parks: A History*, internal and external controversy has always followed the National Park Service. His historical analysis of the Park Service traces the development of the agency's organizational culture. This detailed examination of the roots and growth of the agency provides remarkable insight into current-day resource management and political issues in the national parks.

The book starts appropriately enough in 1872 with the creation of Yellowstone National Park, the world's first national park. There was no model for natural resource protection at that time, although there were two primary foci in the protection of federal lands: wildlife protection (with emphasis on a preferred subset of species) and tourism. The grandeur of Yellowstone captured the American imagination, and although parks were continually added to the system, it was not until 1916 that the National Park Service was officially established by the U.S. Congress with the express purpose of protecting and managing these lands.

The management philosophy of the first two directors of the Park Service, Stephen Mather and Horace Albright, emphasized recreation and tourism by encouraging development of roads and facilities that would bring people to the parks and make it comfortable for them to stay there. The legacy of these agency leaders can still be seen in the national parks today: elegant lodges, large campgrounds, and road systems traversing rugged mountains. This emphasis on tourism has persisted throughout the twentieth century, a fact Sellars points to as a deterrent to the development of science-based resource management within the agency.

Conflicts between science and management were already underway in the 1920s, thanks in part to the efforts of University of California biologist Joseph Grinnell and Park Service wildlife biologist George Wright. Much of the early conflict was focused on general principles of managing large mammal populations. Early biologists favored a reduction in direct management interference with ecosystem processes at a time when agency managers were planting non-native fish in pristine lakes and actively killing predators to enhance ungulate populations. From the 1930s through the 1950s, there was continual philosophical tension between science-based and recreation-based (some would say politically-based) management, and between biologically-trained personnel and the Park Service ranger corps, from whence most of the agency's park superintendents and other leadership were drawn. Sellars points out a sharp contrast between on-the-ground perspectives and administrative policy throughout the twentieth century.

The modern era of resource management dawned with the issuance of the Leopold Report in 1963. This landmark document, in addition to a National Academy of Sciences report in the same year, espoused ecological principles and research as the basis for natural resource management. With the passage of the National Environmental Policy Act in 1969 and increasing environmental awareness among the general public, the Park Service began to incorporate scientific principles into policy and decision-making. The agency developed a small cadre of research scientists and began working more with neighboring agencies and institutions. Despite a bolstered scientific capability, there was a sense that the Park Service was struggling to keep up with a backlog of scientific needs and a new agenda of environmental issues.

As the author brings us into the 1990s, some readers may get a feeling of déjà vu. Conflicts of the 1920s over the management of elk in Yellowstone are equally acrimonious at the end of the century. The poor condition of facilities and the infrastructure of national parks, which was a major issue in the 1950s, is also being addressed today. In a political move, all Park Service scientists were transferred to the Bureau of

Biological Survey in 1940. Remarkably, following the rebuilding of Park Service scientific staff in the 1970s and 1980s, its scientists were removed from the agency in 1993, this time to the National Biological Survey (ultimately subsumed by the U.S. Geological Survey), again reducing the internal scientific capability of the Park Service.

The scope of resource issues considered by the author has a strong emphasis on wildlife. While this may reflect the political reality of the public's disproportionate interest in a few charismatic vertebrate taxa, there are dozens of other stimulating issues that deserve more attention. In addition, the focus is primarily on large national parks, whereas resource management issues in smaller parks are often equally magnified due to fragmentation of the surrounding landscape. Finally, the book contains little discussion about national parks and preserves in Alaska, which contain over half of the land area in the National Park System and have a wide range of issues related to resource protection and to subsistence use of resources by humans. These were all missed opportunities.

Preserving Nature in the National Parks is a highly detailed historical account (including 70 pages of bibliographic notes) and will seem tedious for some readers. Stick with it! The impassioned narrative in the final chapter provides a good synthesis and is a fitting capstone for the preceding six chapters. This volume is a lesson to all agencies of the need to understand organizational culture in order to effectively manage natural resources and initiate change. The book should be required reading for all National Park Service professionals and for anyone who frequently works or recreates in national parks. It provides insight on both positive and negative aspects of modern-day resource management in the agency. Rumor has it that the book has already found a prominent place on the bookshelf of the current Park Service director. This bodes well for the future of the agency if Richard Sellars' message is taken to heart.

—David L. Peterson
USGS Forest and Rangeland Ecosystem Science Center
University of Washington Field Station
Box 352100
Seattle, Washington 98195

White Goats White Lies: The Abuse of Science in Olympic National Park
R. Lee Lyman. 1998. The University of Utah Press. ($29.95)

The role that science and administrative actions play in the management of the natural resources of national parks has been scrutinized in several recent books. This book describes the controversy surrounding the management of mountain goats (*Oreamnos americanus*) in Olympic National Park (ONP). It is a debate that has been previously aired in this journal (c.f. Houston 1995, Lyman 1995) The central issue is whether the mountain goats are 'native' by virtue of the fact that they existed in the Olympic Mountains at some point in the past or whether they are non-native and exist only as the result of a transplant of goats to the Olympic Peninsula in the 1920s. ONP supports the latter position. A second issue, also supported by ONP, is that goat foraging and wallowing is causing serious resource damage to sensitive alpine habitats and the elimination of rare and endemic plant species.

National Park Service (NPS) policy dictates the removal of non-native species in parks. While not uniformly enforced, it is most often addressed when non-native species have been shown to be harmful to park resources. The NPS has removed burros from southwestern parks, feral goats from the Hawaiian parks, and wild boars form the Great Smoky Mountains based on this policy.

Lyman's argument is that ONP's research on mountain goat distribution, population numbers, and resource impacts, and potential historic occupancy in the Olympics has not been objective but rather has been haphazard and sloppy, "founded on faulty logic, incomplete data, and misinterpretation"...(14) making "it appear that...[park researchers] are hiding the truth under a series of white lies in order to strengthen their position that the mountain goats should be eradicated." (15) Lyman does not insist the park's conclusions are wrong, but rather feels eliminating goats now is not warranted based on the evidence produced to date.

The mountain goat controversy in ONP is intriguing and I have used it as an example of human/wildlife interactions in classes. Elements of the controversy as I see them include: a highly charismatic and attractive species, a species that is native in similar alpine habitat less than 65 km away, the unpopular necessity of lethal methods of control, the animal is a game species on lands bordering the park, and the difficulty of assessing the potential ecological impacts of a species which typically occurs in relatively isolated places in the park. All of these issues contribute to socio-political support for the mountain goat and make it difficult for the NPS to act in a region where all resource management actions are scrutinized by a large, environmentally aware urban populace who view the park as their own.

Lyman takes on the controversy primarily by refuting or questioning the park efforts and not by introducing much new evidence. Because the numbers of mountain goats in the park are important in making a case for the urgency of control, Lyman discusses in detail the population census methods used by park scientists. His dissection of the sampling design and re-analysis of the population numbers using different assumptions is interesting. While some of Lyman's comments are valid, he seems to lack an appreciation of the difficulties of counting animals in such an environment or the fact that this was the first detailed census of mountain goats in the park and was thus a learning experience.

He also critiques studies conducted on the impacts of mountain goats on plants. These studies have emphasized the role that mountain goat herbivory had in controlling the relative abundance of different plant species. One aspect of these studies was to analyze the changes observed by comparing paired photos(e.g., pre and post goat occupancy). Lyman looked not so much at the content of the photos but examined the changes in the wording of the captions of the contemporary photos as they appeared in different publications. He often found subtle changes in the caption wording of the more recent photos which suggested that goats were the cause of the photographed impact. Lyman assumes, with no substantiation, that these changes in wording were part of the overall effort by park researchers to garner support for goat control. Again another example, in his opinion, of biased reporting.

ONP historian Susan Schultz's review of the historical evidence relating to mountain goats in

the Olympic Mountains is strongly criticized. Lyman feels "she fails on all counts" (120) to meet her goal of providing a thorough and balanced analysis. Rather, he feels her research is "not thorough and is noticeably biased" (125), and that historic accounts which report mountain goats in the Olympics were missed or purposely omitted from the report.

Archaeologist Randall Schalk's reviews of the archaeological and ethnographic evidence for mountain goats in the Olympics fare much better. Lyman is more confident discussing such evidence. He concludes this chapter by asking two questions: first, what kind of zooarchaeological evidence is necessary to argue convincingly that mountain goats were present in the Olympics prior to 1925? and, secondly, can we conclude from the records that mountain goats were never present in the Olympics? He answers the first question by saying skeletal remains of goats will have to be found. The answer to the second question is more ambiguous. He maintains we cannot conclude goats were never present because there are numerous reasons why prehistoric remains of mountain goats may never be found. He feels that at best, once the requisite time and effort has been spent looking, we can conclude only that mountain goats probably were not present. Following this logic to the extreme would make it virtually impossible for the NPS to conclude any species was non-native.

The question arises that if mountain goats were present at some time in the historical past (e.g., the last 500 years) why weren't they present in the 1920s? The Olympics are good goat habitat, and if goats were there historically their numbers should have been relatively high. What factor was responsible for their extinction prior to 1925? Lyman explains this problem using biogeographic concepts, climate change, and human hunting pressure concentrated in certain areas. He admits that the evidence for any of these factors is at best, indirect. He concludes "while I have not shown...that mountain goats did in fact colonize the Olympics prior to 1925, I find the arguments presented by park biologists that they did not colonize the Olympics to be flawed and not supported by the evidence" (200). As a result, "It would be a major travesty in 'science' to agree to remove goats from the park at this time based on such incorrect information and the usual evidence of the impact of the goat population on the ecosystem" (200).

Lyman, virtually a lone voice in pleading this case in the literature, has support from animal rights advocates and portions of the general public. However their views have been aired in the press and in the courts. Lyman admits that "Virtually all 20th century scientists who...[wrote]...on the mammals of the Olympics...flatly denied the possibility that mountain goats could have been in the Olympics at some time in the past." (152) Likewise, all major external reviews of the park's research program have supported ONP's position.

However, *White Goats White Lies* serves a useful purpose. The park has clearly devoted a lot of time and effort to the study of goats and Lyman does a good job of documenting all of the literature. Some of the errors he reports in analysis and presentation may simply be due to differences in interpretation. However, others should stimulate ONP to reconsider some of its positions, and to more rigorously pursue hypothesis-based research. Conversely, he offers little support for statements like [reviewers of the park's reports]..."did not evaluate that evidence in any manner, nor did they have all the evidence at their disposal." (218)

In the end, I do not believe he makes a convincing case for the fact that ONP researchers were "hiding the truth." Sloppy research techniques at times, yes, conspiracy no. The book will undoubtedly provide more ammunition for a debate that, in my opinion, has gone on too long. For those involved in the issue over the years, the book offers some interesting insights and should provoke some introspection. However, I feel that interest in the book beyond those intimately involved with the Olympics will be limited.

The current EIS on the mountain goat is apparently on hold because of socio-political pressures and Congressional inquiries have surfaced which would seemingly support the retention of mountain goats in the park in lieu of support for wolf reintroduction. Given this situation, Lyman's criticism of the scientific support for or against the mountain goat removal may be a moot point. Social and political criteria may be the most persuasive element of the decision making process regardless of how much, or how little, scientific data there are.

Literature Cited:

Houston, D. B. 1995. Response to "Inaccurate data and the Olympic National Park mountain goat controversy." Northwest Science 69:239-240.

Lyman, R. L. 1995. Inaccurate data and the Olympic National Park mountain goat controversy. Northwest Science 69:234-238.

—R. Gerald Wright
Cooperative Fish and Wildlife Research Unit
University of Idaho, Moscow, ID 83844-1136

Wild To The Last
Charles Pezeshki, 1998. Washington State University Press, Pullman, Washington. ($22.95)

The Clearwater country of north Idaho was once one of the most biologically diverse areas in Idaho and the Northwest and it still possesses great beauty. This mixture of beauty and biological richness has lured humans since long before Europeans "discovered" the country to the present day. Chuck Pezeshki's book, *Wild To The Last*, provides an overview of the ongoing struggle between conservationists, the US Forest Service, the timber industry and communities in north Idaho, which will eventually determine the fate of the last unlogged wildlands in the Clearwater country.

The author contends that the last unroaded wildlands in the Clearwater Country are more valuable as a natural legacy for future human populations than for the logs and minerals that may be extracted from them. *Wild To The Last* lays out Pezeshki's case in three parts; Landscape, People and Crisis. In Part I the reader is taken on a personal tour by the author of selected places in the Clearwater basin. Part II is a number of biographical sketches of some of those who have been engaged in the struggle. In Part III, Crisis, the author lays out the proposition that biologically, things are quickly becoming unraveled in the Clearwater country, and only direct action can alter that reality. The book's epilogue equates what has and is happening to biodiversity in the wild Clearwater with the Jewish Holocaust. Pezeshki has included sketch maps and black and white photos of some of the places he writes about.

It is clear throughout the book that Pezeshki is deeply moved by the country he writes about, yet his passion for the wild Clearwater alone is not enough to make this a great book. While some sections are well written, others are not. The "Landscape" is hodgepodge of vignettes that describe various places, some scarred by roads and logging, others still unroaded but up for grabs. Yet, taken altogether the picture painted in Part 1 is confused, unfocused. It is as if no one planned the excursion through the Clearwater country. There is no compass to direct the reader to a specific point. One simply cannot tell when they have arrived at the place Pezeshki intended them to reach. Like the author, I stumbled through his landscapes, always a bit lost, even given the maps and photographs. When the trip ended my main recollection was of the sad tale of the shooting of a mountain goat that had become habituated to humans. Not so much because it was such an unfortunate occurrence, but rather because the other sketches failed almost completely to grab and hold my attention.

Better written and more interesting are the "People" of *Wild To The Last*. In Part II Pezeshki presents the reader with short profiles about some of the individuals involved in the struggle over the future of the country. This section works better because these are the subject's own stories, often in their own words. The reader hears from the loggers, agency folks, academicians and environmental activists, all of whom take a cut at explaining what is important about the Clearwater country and why. One of these sketches is particularly good. "Rowdy's" story is that of a soon to be unemployed mill worker from the logging town of Grangeville. Rowdy's future is to be retrained then move out of the country, hopefully to a new job. Pezeshki explores with Rowdy the chain of events that lead to his inevitable dislocation. One soon realizes that there is more than the loss of wildlands and wildlife when land managers fail in their jobs.

The third part of the book, "Crisis," is the author's reality of why the book was written. In fact it is almost as if "Crisis" was written first, then Parts I and II to fill out the volume. Unfortunately it also suffers from a failure to focus on a central theme. For instance, "Children's Crusade" is a rambling account of the environmental activists trying to prevent the roading and logging of the Cove/Mallard area on the Nez Perce National Forest. It may be that the section seemed scattered because the situation was fluid and there really was no organization to the civil disobedience activities that took place at Cove/Mallard. Nevertheless, the account is distracting and seems out of context with the premise of this section of the book.

Ironically, it is also in Part III that the reader will find the most salient account of Pezeshki's vexations with the state and federal land managers and their partners in the timber industry. The sections on the "salvage logging rider" and the massive mud slides that took place on the

Clearwater and Nez Perce Forests in late 1997 accurately portray the culpability shared by the timber corporations and the agencies in perpetuating industrial scale logging and roading, and the resultant impacts to wildlands, wildlife and water quality in the Clearwater Country.

Wild To The Last is an awkward book. I found the book's preface the tightest, best written and most memorable part of the book. Paradoxically, it also has the least to do with the author's cause of rallying support for the wildlands of northern Idaho, a truly good and just cause. The wandering nature of the book makes it difficult to pay close attention, to stay involved with the underlying message of the book. I fear this aspect alone will cause readers, outside the world of committed conservationists, to put the book aside. And that would be unfortunate because the story and tragedy of what has and is happening to the Clearwater Country is important to us all.

—Marv Hoyt
1307 Herring Street
Idaho Falls, Idaho

NORTHWEST SCIENCE

Information for Authors

Scope of Articles

The pages of *Northwest Science* are open to original and fundamental research in the basic, applied, and social sciences. All submissions are refereed, usually by two reviewers. Papers are welcome from authors outside of the Pacific Northwest, but at least one author of any paper considered for publication must be a member of the Northwest Scientific Association.

Manuscripts

General Instructions: Submit four copies of the paper (including tables and figures) to the Editor. Manuscripts should be typewritten on 8-1/2 x 11 inch paper, double-spaced throughout (including abstract, acknowledgments, literature cited, tables, and legends for figures); ample margins must also be provided. Unnecessary footnotes should be avoided.

The manuscript should consist of sections in the following sequence:

- Title Page
- Abstract
- Text (Introduction through Acknowledgments)
- Literature Cited
- Footnotes
- Tables
- Figure Legends
- Figures

Maximum article length for papers published in *Northwest Science* is 16 journal pages. Two typed pages are approximately equal to one journal page.

Numerals will be used to indicate footnotes unless such usage would be confused with numerical data. In this situation, lowercase letters should be used. Do not break, or hyphenate, words at the ends of lines. Words to be italicized should be typed in italics.

The format and style of manuscripts should conform to general usage in recent issues.

Title Page: The first page of the manuscript should contain:

- Author's name (or names)
- Institutional address from which manuscript emanated, including city, state or province, postal code
- Title of paper
- Running head
- Total number of text figures and tables
- *Correspondence to:* List name, full address, telephone number, fax number, and e-mail address of the individual to whom correspondence should be sent.

Abstract: The purpose of an abstract is to briefly summarize the study so it is quickly accessible to the general readership of the journal. The abstract, written in complete sentences and not exceeding 250 words, should precede the text on a separate page. Authors are reminded of the diverse disciplines and readership served by the journal. With this in mind the abstract should have three parts of unequal length. First, the abstract should begin with a statement of the purpose of the study that indicates *why the study was undertaken.* Next the experimental design or approach should be stated and the *results summarized.* The abstract should end with a sentence or two on the larger significance of the research. Authors are strongly encouraged to give the abstract proper attention.

Text: Literature citations within the manuscript text should contain the author's name and year of publication, using formats A and B.

- Format A:
  ...studied by Jones (1978)...
  ...studied by Smith and Brown (1979)...
  ...studied by Smith et al. (1980)... (if more than two authors in a citation)
- Format B:
  ...was previously investigated (Smith 1965, Jones 1971, Harris 1982)...
  ...results of other investigations (Smith 1966, 1970; Jones 1973; Brown 1974)...

Numbers from one to nine will be spelled out, while arabic numerals will be used for numbers 10 and larger. Exceptions to this rule are: 1) a series of "mixed" numbers (e.g., 14 elk, 35 deer, 2 bobcats, and 1 bear); 2) when the number immediately precedes an abbreviation for a standard unit of measure (e.g., 3 g, 18 mm, 300 m^2). Numerals will also be used for dates, times, page numbers, and percentages.

Present all data in international (SI) units. English equivalents may be added parenthetically. Use the 24-hour clock (0600 and 2230) and continental dating (17 November 1986).

On first mention, a species should be designated by common name followed by systematic binomial (italicized). Common names for species should not be capitalized except when derived from a proper name. Thus, "mountain hemlock" or "white-crowned sparrow," but "Douglas-fir" or "Clark's nutcracker." For abbreviations and forms of titles for serial publications, follow the BIOSIS List of Serials. Consult with the Council of Biology Editors *CBE Style Manual,* 4th ed., for general information on manuscript preparation.

Literature Cited: Only the *first letter* of the *first word* of journal articles, technical reports, theses, etc. are capitalized. First letters of *major words* in book titles are capitalized. All authors of a title are listed in the bibliographic citation ("et al." is used only in the body of the text).

Citation of unpublished reports is discouraged. Rather, cite the sources as a personal communication from the senior author (P. W. Smith pers. comm.).

Citations should be double-spaced and listed in alphabetical order at the end of the article. Listed below are some typical citations.

Journal articles

Broadbooks, H. E. 1970a. Home range and territorial behavior of the yellow pine chipmunk *Eutamius amoenus.* J. Mammal. 51:310-326.

_____. 1970b. Populations of the yellow pine chipmunk, *Eutamius amoenus.* Amer. Midl. Nat. 83:472-488.

Ceska, A., and H. Romer. 1971. A computer program for identifying species group. Vegetatio 20:48-73.

Grizze, J. E., C. F. Starmer, and G. G. Kuch. 1969. Analysis of categorical data by linear models. Biometrics 25:489-504.

Monographs or books

Jennings, H. S. 1906. Behavior of the Lower Organisms. Columbia University Press, New York.

Papers in proceedings or symposia

Ryland, J. S. 1975. Parameters of the lophophore in relation to population structure in a bryozoan community. *In* H. Barnes (ed.) Proc. 9th Eur. Mar. Biol. Symp., Aberdeen University Press, Aberdeen. Pp. 363-393.

Theses, dissertations, personal communications, and articles in press

Donald, D. B. 1971. The limnology of the plankton of three temporary pons in Alberta. University of Calgary, Calgary. M.S. Thesis.

Wiser, H. C. 1961. Decomposition and homogeneity of continua on 2-manifolds. University of Utah, Salt Lake City. Ph.D. Dissertation.

Dunwiddie, P. W. In Press. Dichotomous key to conifer foliage in the Pacific Northwest. Northw. Sci.

Technical Bulletins

Daubenmire, R., and J. B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. Wash. Agric. Exp. Sta. Tech. Bull. 60. Washington State University. 210 p.

Goodwin, J. G., Jr., and C. R. Hungerford. 1979. Rodent population densities in pine forests. USDA For. Serv. Res. Pap. RM-214. Rocky Mtn. For. Range Exp. Sta., Fort Collins, Colorado. 39 p.

Footnotes: Footnotes to the text should be limited as much as possible and must be numbered consecutively. The corresponding numbers must be clearly indicated in the text.

Tables: All tables must be cited in the text, but typewritten (double-spaced) on separate pages. When submitting tables electronically, they should be presented in the simplest tabular format possible, and placed in a separate file from text.

Figures: All figures must be cited in the text. To achieve greater published fidelity, it is preferable for the printer to work directly from original photographs or drawings. Thus, original artwork or black & white glossy prints of photographs must be submitted for reproduction. When sent, be sure to include enough firm backing (e.g., lettering board) to protect them from damage. Artwork and lettering should be large enough (but not overly large) to provide clarity after a 50% reduction in size for printing. *The author's name*

and figure number should be penciled on the back of each illustration. Provide a scale for distance on map illustrations. Legends for illustrations should be typed as a group and placed on a separate page. In reference to figures and tables the words "Figure" and "Table" should be spelled out and capitalized as follows:

- ...experimental sites as indicated in Figure 2...
- ...correlation between temperature and biomass (Table 3)...

Artwork, photography, and camera ready art cannot be returned to the author.

Editing—The Editor reserves the right to edit manuscripts for grammatical correctness and clarity.

Submission of Final Copy—Manuscripts accepted for publication must be submitted in electronic copy as well as hard copy. Authors will receive instructions from the Editor regarding acceptable word processing software.

Publication Agreement—Each author or group of authors must sign a Publication Agreement provided by the Editor before their submission will be published in the journal.

Galley Proofs and Reprints—One set of proofs will be sent to the indicated author for correction shortly before publication; proofs should be returned to the Editor within *three days* of receipt. Authors should inform the Editor of any change of address for handling proofs. Reprints must be ordered when the proofs are returned. A schedule of reprint prices will be sent to the author with the proofs. Allow 8 weeks for delivery after the journal issue carrying the article appears.

Page Charges—Page charges are currently $60 per printed page. A bank draft, money order, or institutional purchase order to cover page charges and optional reprints should be submitted to the Editor upon return of galley proofs.

Correspondence—All correspondence regarding manuscripts will be between the corresponding author and Editor.

Reviewers—The associate editors reserve the right to select reviewers of their choice.

Revised November 1996

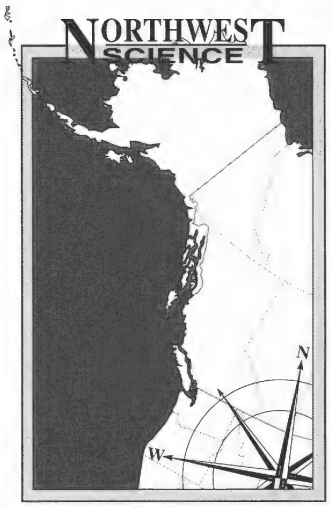
Join
The Northwest Scientific Association

A membership in the Northwest Scientific Association carries several benefits including subscription to the quarterly professional journal, *Northwest Science.*

Northwest Science is a refereed journal that has published original research in the basic, applied, and social sciences for over seventy years. Distributed throughout the Pacific Northwest, the United States, Canada, and more than fifty countries, *Northwest Science* reaches an international audience.

Members of the Northwest Scientific Association help support research and scholarship across a wide range of disciplines. Members also help underwrite scientific investigations through the Association's Research Grant Fund for graduate and undergraduate students. The annual meeting of the Association includes invited symposia as well as contributed paper sections.

Membership in the Northwest Scientific Association includes a subscription to *Northwest Science* and can be obtained by paying the appropriate dues (listed below). In addition to regular quarterly issues, members also receive occasional special issues focusing on particular scientific topics.



Inquiries concerning submissions for the journal should be directed to the Editor, whose address is listed in the inside front cover of the journal.

Clip and mail

I would like to join the Northwest Scientific Association and receive the quarterly publication *Northwest Science.*
Enclosed is a check or money order for membership dues for one year as a(n):

- ❑ Regular member ($25.00)
- ❑ Institutional member ($40.00)
- ❑ Sustaining institutional member ($100.00)
- ❑ Student member ($10.00)
- ❑ Sustaining member ($40.00)

Name

Address

City State/Province Postal Code

Dues are payable in advance and by calendar year. Please make all checks payable to the Northwest Scientific Association in U.S. currency and send to Northwest Science, c/o Washington State University Press, PO Box 645910, Pullman, WA 99164-5910, USA.

Honorary Life Members

Ewart M. Baldwin
L. C. Cady
Robert L. Carr
R. A. Diettert
Bruce V. Ettling
William K. Ferrell
Nancy J. Grunewald
Philip Haddock
Kenneth Hammond
Adolf Hecht
Caroline Hooper
Kenneth V. Kardong
G. Brooks King
Rufus W. Kiser
Denis P. Lavender
Lewis and Clark High School Library (In memory of Thomas Large and J. G. McCracken)
Joseph W. Mills
Richard J. Naskali
Frank D. Nicol
David L. Peterson
Charles Gardner Shaw
Oscar Sziklai
Robert F. Tarrant
Richard B. Walker
D. J. Wort

1998 Institutional Members

Boise State University, Boise, ID
British Columbia Institute of Technology, Burnaby, BC, Canada
Central Oregon Community College, Bend, OR
Central Washington University, Ellensburg, WA
Centralia College, Centralia, WA
College of Idaho, Caldwell, ID
Eastern Montana College, Billings, MT
Eastern Oregon State College, LaGrande, OR
Eastern Washington University, Cheney, WA
Edmonds Community College, Lynnwood, WA
The Evergreen State College, Olympia, WA
Grays Harbor College, Aberdeen, WA
Green River Community College, Auburn, WA
Idaho State University, Pocatello, ID
Lewis-Clark State College, Lewiston, ID
Lewis and Clark College, Portland, OR
Linfield College, McMinnville, OR
Montana College of MIning Science & Technology, Butte, MT
Mt. Hood Community College, Gresham, OR
North Idaho College, Coeur d'Alene, ID
Northern Montana College, Havre, MT
Oregon State University, Corvallis, OR
Pacific Lutheran University, Tacoma, WA
Pacific University, Forest Grove, OR
Peninsula College, Port Angeles, WA
Portland State University, Portland, OR
Simon Fraser University, Burnaby, BC, Canada
Skagit Valley College, Mount Vernon, WA
Spokane Falls Community College, Spokane, WA
University of Alaska, Fairbanks, AK
University of Alberta, Edmonton, AB, Canada
University of British Columbia, Vancouver, BC, Canada
University of Idaho, Moscow, ID
University of Montana, Missoula, MT
University of Oregon, Eugene, OR
University of Victoria, BC, Canada
University of Washington, Seattle, WA
Walla Walla College, College Place, WA
Washington State University, Pullman, WA
Western Washington University, Bellingham, WA
Whitman College, Walla Walla, WA

1998 Sustaining Individual Members

James K. Agee, Redmond, WA
Neil B. Armantrout, Eugene, OR
Donald J. Bedunah, Lolo, MT
Kevin R. Brown, Victoria, BC
Richard A. Cellarius, Olympia, WA
Kermit Cromack,Jr., Corvallis, OR
Diane S. Doss, Sequim, WA
George W. Douglas, Duncan, BC
Larry A. Drew, Rathdrum, ID
Rich T. Easterly, Tenino, WA
Paul A. Fishman, Portland, OR
Robert W. Gray, Sumas, WA
Robert E. Gresswell, Corvallis, OR
Frederick C. Hall, Portland, OR
Paul E. Hammond, Portland, OR
Donald P. Hanley, Seattle, WA
Randy Hein, East Wenatchee, WA
Jan A. Henderson, Mountlake Terrace, WA
Francis R. Herman, Fairbanks, AK
Barry L. Keller, Idaho Falls, ID
Karel Klinka, Richmond, BC
William N. Laval, Clarkston, WA
Giles W. Maloof, Boise, ID
Paul A. McDaniel, Moscow, ID
Howard R. Panik, Carson City, NV
Mauri S. Pelto, Dudley, MA
Steven K. Rust, Boise, ID
Penny Schaefer, Lacey, WA
Edward G. Schreiner, Port Angeles, WA
Charles G. Shaw, Auke Bay, AK
Dale Stradling, Cheney, WA
Kenneth C. Swedberg, Cheney, WA
Robert F. Tarrant, Corvallis, OR
David H. Wagner, Eugene, OR
James & Nancy Weber, Corvallis,OR
Andrea Woodward, Seattle, WA

Any member noticing information on this page that is outdated or incorrect should please bring this to the attention of the Editor.

WSU PRESS Washington State University Press
PO Box 645910
Pullman, Washington 99164-5910 USA

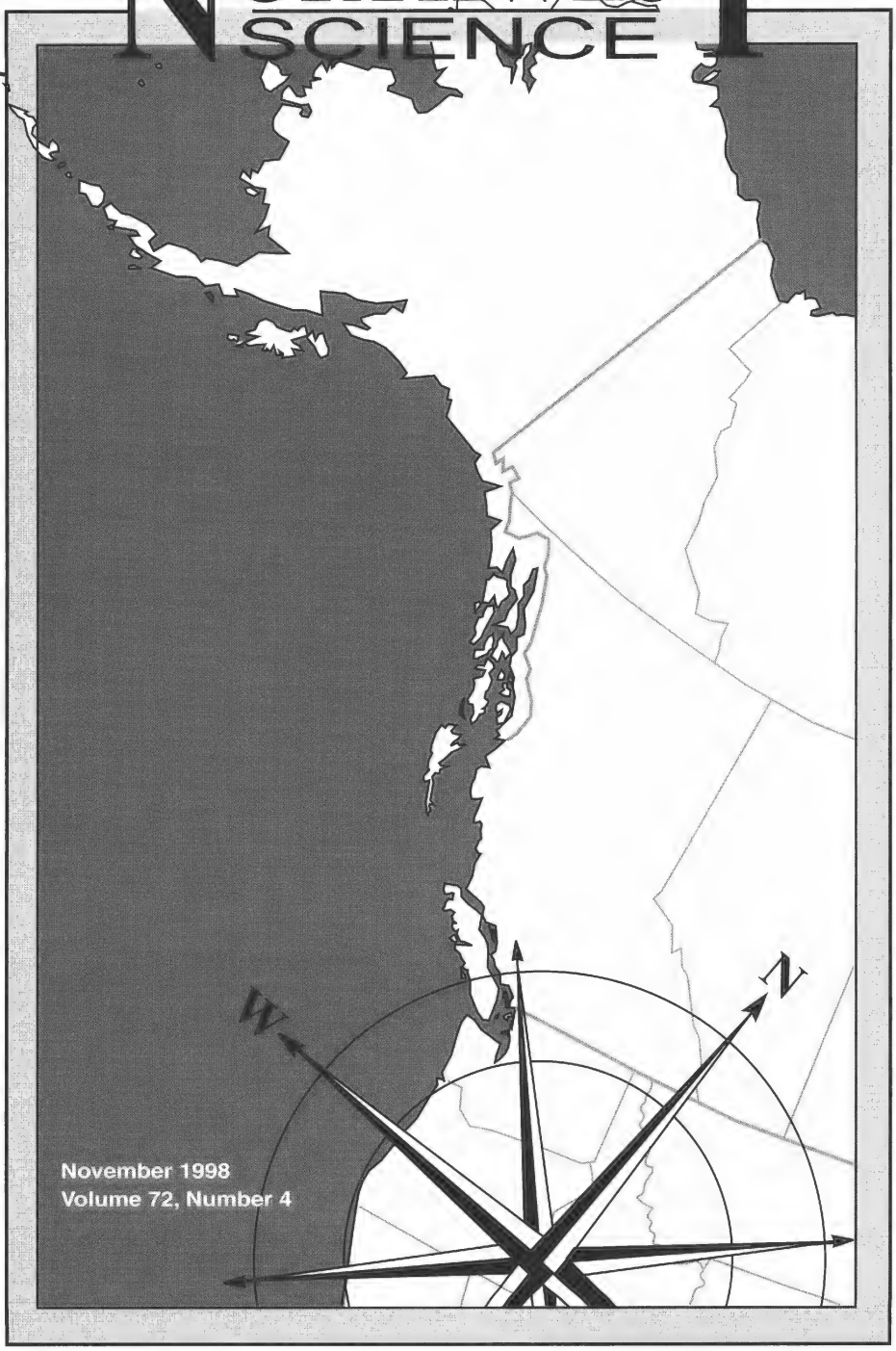
Nonprofit Organization
U.S. Postage
PAID
Pullman, WA
Permit No. 1

Northwest Science

Quarterly Publication of the Northwest Scientific Association

Papers published in **Northwest Science** are indexed in *Current Contents, Science Citation Index, Biological Abstracts, The Zoological Record, Recent Literature Supplement to The Auk, Abstracts in Anthropology, Bibliography and Index of Geology, Chemical Abstracts, Bibliography of Agriculture, Forestry Abstracts, University Microfilms, Geo Abstracts, GEOBASE,* and *Cambridge Scientific Abstracts, Elsevier BIOBASE/Current Awareness in Biological Sciences.*

NORTHWEST SCIENCE



November 1998
Volume 72, Number 4

Northwest Scientific Association

(Founded 1923)

The Northwest Scientific Association, an affiliate of the American Association for the Advancement of Science, is an association representative of the basic and applied sciences and of social sciences.

Membership in the Northwest Scientific Association, which includes a subscription to *Northwest Science,* is open to individuals for $25 per year ($10 per year for students). Institutional membership, $40 per year. Sustaining membership, $40 per year for individuals and $100 per year for organizations, institutions, or agencies. Subscriptions are for the calendar year only.

Send membership dues, changes of address, and requests for undelivered issues to the Treasurer.

The Northwest Scientific Association is a 501-C(3) tax status organization.

Editor of *Northwest Science*

Edward G. Schreiner
USGS/BRD, Olympic Field Station
600 E Park Avenue
Port Angeles, Washington 98362
Telephone: 360-452-4501 x244
Fax: 360-452-0335
Internet: Ed_Schreiner@nps.gov

Officers of the Association

President Theodore B. Thomas
USDI Fish & Wildlife Service
Olympia, Washington (2000)*

Past President Richard Cellarius
The Evergreen State College
Olympia, Washington (1999)

Secretary Margaret O'Connell
Department of Biology MS-72
Eastern Washington University
Cheney, Washington 99004 (2000)

Treasurer David H. Hansen
Department of Biology
Pacific Lutheran University
Tacoma, Washington 98447 (2000)
Telephone: 253-535-7565
Fax: 253-536-5055
Internet: hansendh@plu.edu

Book Review Editor
Randall C. Morris
Environmental Science and Research Fndn.
101 S. Park Ave./PO Box 51838
Idaho Falls, ID 83405-1838
Telephone: 208-525-7053, Fax: 208-525-7036
e-mail: morrisr@esrf.org

Trustees:

Ross Black
Eastern Washington University
Cheney, Washington (1998)

Leonard Broberg
University of Montana
Missoula, Montana (2001)

Herbert Brown
Western Washington University
Bellingham, Washington (1999)

Sally Hacker
Washington State University
Vancouver, Washington (2001)

Charles Halpern
University of Washington
Seattle, Washington (2000)

Miles Hemstrom
USDA Forest Service
Portland, Oregon (1999)

Kenneth V. Kardong
Washington State University
Pullman, Washington (2001)

Barry L. Keller
Idaho State University
Pocatello, Idaho (1999)

John Koprowski
Willamette University
Salem, Oregon (2000)

Paul A. McDaniel
University of Idaho
Moscow, Idaho (2000)

Kurt Othberg
Idaho Geological Survey
Moscow, Idaho (2000)

Tim Reynolds
Environmental Science and Research Foundation
Idaho Falls, Idaho (2000)

Roger Rosentreter
Bureau of Land Management
Boise, Idaho (1999)

Steve Sillett
Humboldt State University
Arcata, California (2001)

Darlene Zabowski
University of Washington
Seattle, Washinton (2001)

*Term of office expires in the year given in parentheses.

© 1998 by the Northwest Scientific Association. All rights reserved.

November 1998 Volume 72, Number 4

NORTHWEST SCIENCE

Editor	Edward G. Schreiner	USGS/BRD—Olympic Field Station, Port Angeles
Managing Editor	Nancy J. Grunewald	Washington State University
Indexer	Caroline Hooper	
Associate Editors		
Anthropology	R. Lee Lyman	University of Missouri—Columbia
Aquatic Biology	Gary L. Larson	U.S. Geological Survey—Corvallis
Botany	Eldon H. Franz	Washington State University
Mathematics & Computer Applications	Steven J. Ghan	Battelle Pacific Northwest Labs—Richland
Forestry	Michael C. Feller	University of British Columbia
Geology & Geography	David R. Gaylord	Washington State University
Soils	Robert L. Edmonds	University of Washington
Wildlife Biology	Patricia J. Heglund	University of Idaho
Zoology	Richard B. Forbes	Portland State University
Book Reviews	Randall C. Morris	Envir. Sci. & Res Fdn.—Idaho Falls

ISSN #0029-344X

CONTENTS

Memoriam to Ron Taylor

Announcements

239 Pacific Salmon Spawner Escapement Goals for the Skagit River Watershed as Determined by Nutrient Cycling Considerations—**John H. Michael Jr.**

249 Management and Condition of Watersheds in Southeast Alaska: The Persistence of Anadromous Salmon—**Mason D. Bryant and Fred H. Everest**

268 Control of Scot's Broom (*Cytisus scoparius* (L.) Link.): The Relative Conservation Merits of Pulling versus Cutting—**Joel G. Ussery and Pam G. Krannitz**

274 Root Growth of *Eucalyptus pauciflora* Sieber ex Sprengel ssp. *pauciflora* on Mount Stirling, Southeastern Australia—**Reese Halter**

283 Pacific Yew (*Taxus brevifolia* Nutt.) Growth and Site Factors in Western Oregon—**John Duff Bailey and Leon H. Liegel**

293 Small Mammal Abundance in Riparian and Upland Areas of Five Seral Stages in Western Oregon—**Douglas M. Gomez and Robert G. Anthony**

303 Snag Recruitment in Subalpine Forests—**Paul T. Flanagan, Penelope Morgan, and Richard L. Everett**

Northwest Science Forum

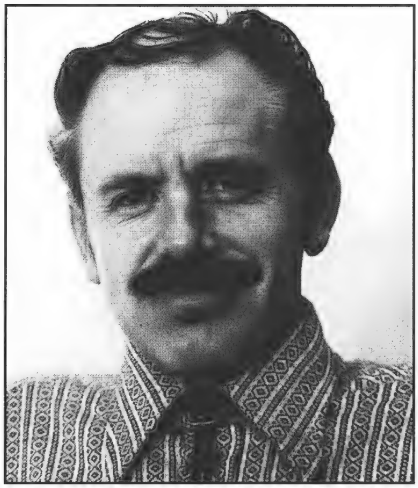
310 Marbled Murrelets *Have* Declined in Alaska—**John F. Piatt**

315 The Challenge of Evaluating Population Trend for Conservation Management: Marbled Murrelets in Alaska—**Gregory D. Hayward and George C. Iverson**

Book Review

320 *Not Just Trees: The Legacy of a Douglas-fir Forest* by Jane Claire Dirks-Edmunds—**reviewed by David H. Hansen**

IN MEMORIAM: RONALD J. TAYLOR, 1932-1998



Ronald J. Taylor, Professor of Biology Emeritus at Western Washington University, passed away on 16 August 1998 at his home in Bellingham, Washington. Ron was diagnosed with cancer in early 1997, and he made heroic efforts to win this battle for his life. Ron held much optimism in the cancer treatments, and with his wife Gloria providing loving attention and encouragement he was able to live beyond the estimates of the medical professionals. Ron was born in Victor, Idaho on 16 October 1932 and grew up on a ranch in the foothills of the Teton Mountains and the Snake River where his interest in the natural world developed. Ron obtained a B.S. degree (1954) in conservation at Idaho State University, then became an officer and pilot (1954-1959) in the Air Force; he later earned the M.S. degree (1960) in botany at the University of Wyoming and Ph.D. (1964) in botany and genetics at Washington State University. Ron joined the Biology Department at Western Washington University in 1964 and taught general biology, evolution and botany classes until his retirement in 1992. He was Chairman of the Biology Department from 1984 to 1992.

Ron was completely dedicated to his family and to his profession. The teaching of biology to undergraduate and graduate students was of the highest priority, and he took particular satisfaction in the fifteen graduate students who completed M.S. degrees in biology under his guidance at WWU. Considering the influence that his students now have in promoting environmental education and conservation biology in the Pacific Northwest, this legacy continues Ron's commitment to the protection of wildlife and their habitats. Ron was instrumental in the development of several conservation management habitats: Sehome Hill Arboretum on the WWU campus, the Beaver Creek Natural Resources Conservation Area on the outskirts of Bellingham, and other more distant sites like subalpine meadows on Chowder Ridge (Mt. Baker) and Chopaka Peak (Okanogan Highlands). Ron's research interest resulted in 46 scientific articles, and he also published six popular field guides to plants. The last book, completed during his illness, is "Desert Wildflowers of North America" (1998) and includes the Mojave, Sonoran, Painted, Chihuahuan, and Great Basin Deserts. Ron was a skilled nature photographer and his vast collection of slides (used in classroom lectures or public meetings, and to illustrate the field guides) has been donated to the Biology Department Herbarium at Western Washington University.

Ron loved the beauty and serenity of sagebrush country and those magnificent mountains that protect his favorite retreat, the subalpine flower gardens. These were the wild places that attracted this systematic biologist, and he would fondly devote much time and effort to study the evolution and reproductive strategy of montane and subalpine plants. We traveled together

on many hiking trails in the North Cascades and the slopes of Mt. Baker, and I see him now in the heather meadows of Yellow Aster Butte with his camera focused on a grape fern or climbing a steep cliff above Skyline Divide to reach the meadows of Chowder Ridge and then collecting samples of sedges requested by a colleague in Colorado. He was able to share this combination of rigorous science and appreciation of nature during numerous fieldtrips with many civic and conservation oriented groups like the Washington Native Plant Society, North Cascades Institute, Audubon Society, Nature Conservancy, and the American Rock Garden Society. He was particularly proud of his long time membership in the Northwest Scientific Association and their award to him of Honary Lifetime Member because of his valuable contributions to biological education, research and conservation in the Pacific Northwest.

In his retirement years Ron developed a keen appreciation of birds, and his backyard provided a glorious garden of trees, shrubs, and flowers with a beautiful pond that attracted a large assortment of bird species. He and his wife Gloria would sit on the porch or living room with binoculars in hand and find enormous enjoyment in the lively antics of this avian assemblage.

Ron was very independent, and sometimes competitive, but he also was kind and humorous. We will always remember his talent at whistling a tune while he strode down the hall or even performing a song with great skill and enthusiasm in the company of close friends, and who can forget those delicious pancakes covered with chokecherry syrup that he would always share during camping trips to sagebrush country. Ronald J. Taylor had a remarkable life, and as he concludes in his personal autobiography "It has been a good life at the best of times!" It has been a privilege for all of us to share this great adventure and know this gifted and talented man.

Herbert Brown
Biology Department
Western Washington University
Bellingham, Washington

Announcements

The Northwest Scientific Association is soliciting nominations for individuals to serve as trustees on the Governing Board. Trustees are selected for their appreciation of scientific research and recognized ability in their chosen fields. If you would like to submit a nomination, please contact:

Dr. Paul A. McDaniel
Soil Science Division
University of Idaho
Moscow, ID 83844-2339
phone: 208-885-7012
email: pmcdaniel@uidaho.edu

John H. Michael Jr., Washington Department of Fish and Wildlife, 600 Capitol Way N, Olympia, Washington 98501-1091

Pacific Salmon Spawner Escapement Goals for the Skagit River Watershed as Determined by Nutrient Cycling Considerations

Abstract

Wild populations of Pacific salmon (*Oncorhynchus spp.*) in Washington State are generally at low levels compared to populations that were likely present before the arrival of Euro-Americans in the Pacific Northwest. Habitat loss, the introduction of non-native stocks and species, and overfishing have all contributed to the decline. Historically, huge numbers of salmonid carcasses provided entire watersheds with nutrients derived from the ocean. Diminished populations and transport of these nutrients out of watersheds has caused a nutrient deficiency compared to times when populations were large. This nutrient deficiency may be hampering recovery of salmon and other animal populations. Beginning with the premise that the Pacific Northwest ecosystem evolved to fully utilize massive numbers of spawning salmon, I estimated the biomass of salmon carcasses necessary to support nesting song birds, wintering bald eagles, and salmonid smolt production in the Skagit River watershed in Washington. The proposed spawner escapement goals thus estimated are 150% to 680% higher than current spawner escapement goals for salmon in the watershed. The justifications for these proposed goals include comparison with escapement goals used in other watersheds, the actual uptake of marine-derived nutrients by fish, the impact of increased escapement on subsequent smolt production, and actual relationships between adult spawners and smolts in less intensively fished streams. Actual attainment of these goals will need to consider the physical condition of the watershed and its ability to retain and cycle the nutrients and the social and economic disruption to fisheries that may result from allowing more fish to survive to adulthood and spawn.

Introduction

Declines of wild salmonid populations in the Pacific Northwest have focused attention on the region, its fish populations, and changes in aquatic and terrestrial habitat which threaten the continued existence of large anadromous salmonid populations (Nehlsen et al. 1991, Palmisano et al. 1993, McIntosh et al. 1994, Wissmar et al. 1994). The ecosystem in which Pacific salmon (*Oncorhynchus spp.*) evolved was one where they transported substantial amounts of nutrients from marine to fresh water when they returned to their natal watershed to spawn and die. Kline et al. (1990) and Kline et al. (1993), using isotopes of carbon and nitrogen, documented that salmon carcasses provided nutrients which "fed" stream and lake ecosystems. At Karluk Lake, Alaska, Koenings and Burkett (1987) suggested that reduced nutrient input resulting from fewer spawners contributed to the inability of the sockeye salmon population to increase to historic levels. Other studies have shown that the addition of nutrients to aquatic systems increased juvenile salmon size and increased the abundance of adults (Holtby et al. 1990, Johnston et al. (1990), Kyle (1994), and Stockner and MacIsaac (1996).

Before commercial canneries, with their product distribution networks which transport preserved salmon flesh far from the home watershed, most of the salmon biomass harvested by animals or people remained in the watershed. Waste was generally returned to the river, the animals and people lived and died in the watershed, and so on. Consequently, it seems reasonable that the watersheds of the Pacific Northwest evolved to capture and use the massive annual influx of marine nutrients brought by anadromous salmonids.

Salmon carcasses are utilized at every level of the food chain, and then cycle through the system by consumption as prey items (Bilby et al. 1996). Willson and Halupka (1995) hypothesized that anadromous fish in Pacific Northwest streams are keystone animals of the ecosystem. Salmonid presence and abundance has important consequences for the distribution and abundance of terrestrial vertebrates. Sibatani (1996) presented the idea that one major ecological role of Pacific salmon is to transport nutrients, particularly phosphates and nitrates, from the ocean to the forest lands surrounding the northern Pacific Ocean range of the fish. He used calculations which showed that riparian forest birds incorporate a significant portion of nutrients from salmon carcasses by

© 1998 by the Northwest Scientific Association. All rights reserved.

eating insects which had fed on the carcasses. Hilderbrand et al. (1996) calculated that 33% to 90% of the metabolized carbon and nitrogen in museum specimens of Columbia River drainage grizzly bears (*Ursus arctos horribilis*) collected before dam construction was obtained from salmon. Ben-David et al. (1997) concluded that mink (*Mustela vison*) in southeast Alaska relied on salmon carcasses as a food source during the autumn spawning runs. Hunt et al. (1992) and Stalmaster and Kaiser (1997) estimated the amount of salmon carcasses consumed by bald eagles (*Haliaeetus leucocephalus*) wintering on western Washington rivers. Both papers noted that overall numbers of wintering bald eagles were directly related to actual availability of salmon carcasses. These studies allow for a quantification of salmonid carcasses needed within an ecosystem. Cederholm et al. (1989) documented a wide variety of terrestrial mammals and birds that feed on salmon carcasses, but did not quantify the amount of usage.

Michael (1995) demonstrated a direct correlation between the biomass of spawning pink salmon (*O. gorbuscha*) and the resultant production of adult coho salmon in the Skagit River. Ongoing studies by the Washington Department of Fish and Wildlife (WDFW) have further supported this relationship by showing that coho salmon smolt production in the Skagit River was strongly and directly correlated to the number of pink salmon spawning the year before smolt emigration (D. Seiler, WDFW Biologist, pers. comm.). Therefore, relating the biomass of smolts produced in a system to the biomass of carcasses necessary to produce them could provide an escapement goal which considers the "needs" of the ecosystem across species rather than the traditional single species spawner-recruit models.

To effectively manage any renewable resource, it is necessary to define and protect a specified level of reproducing individuals—the escapement goal in fisheries. This level of reproduction is also used to measure the success of a management strategy. Presently, most fish management strategies for Washington salmon stocks maximize the production of harvestable fish. Increasing the escapement goals will, at least in the short term, lower harvest levels, and stakeholders generally oppose attempts to reduce harvests without justification. Larkin and Slaney (1997) reviewed salmonid escapements and resultant fish production in British Columbia, and concluded (pg. 22) "... enough information has been gathered ... to conclude that wild stocks may be at risk and, therefore, we argue for an immediate management response". WDFW is developing a new set of policies to manage wild salmonids. Among the goals of these policies will be increased spawner escapements. Current spawner escapements are based on some variant of Maximum Sustained Yield with considerations of economics and other non-biological aspects as desired by the managers (Wright 1981). Presently, the escapement goal does not consider the nutrient contribution of adult spawners to the ecosystem.

The goal of this paper is to present a method for determining the spawner escapement goal for Pacific salmon by attempting to quantify the number and biomass of salmon carcasses required to support nutrient needs of specific segments of the ecosystem. The Skagit River watershed was used as an example to test how the method might affect spawner escapement goals. The first step was to calculate the amount of food necessary to: (1) produce a given biomass of juveniles of selected anadromous salmonids with extended freshwater rearing, (2) support overwintering bald eagles, and (3) support nesting insectivorous birds. The estimated spawner biomass was then compared with recent levels of spawner biomass observed in the Skagit River. Spawner escapement goals developed using this method offer a scientific basis for increasing spawner levels but they underestimate actual ecosystem needs because they exclude species such cutthroat trout (*O. clarki clarki*), native char (*Salvelinus spp.*), sturgeon (Acipenseridae), lampreys (Pteromyzontidae), and smelt (Osmeridae) for which little information on numbers and biomass of spawners exists. Estimates also do not include quantities of marine-derived nutrients needed by herptiles, mammals, birds other than the riparian zone nesters and wintering bald eagles, insect-consuming invertebrates, or plants.

Study Area and Methods

This study is based on the Skagit River watershed in Washington, USA. Michael (1995) describes the Skagit River watershed and salmon populations and biomasses. An estimated 905.4 km of stream are accessible to anadromous fish in the Skagit River watershed (Johnson 1986).

Spawner escapement goals which recognize ecosystem nutrient needs can be expressed as:

$$\Sigma B = B_1 + B_2 + B_3 + \ldots B_n$$

Where:

ΣB= the total biomass of salmonid carcasses necessary to supply nutrients to the ecosystem

B_1= carcass biomass necessary to support chinook salmon (*O. tsawytscha*), coho salmon (*O. kisutch*), and steelhead trout (*O. mykiss*) smolts

B_2= carcass biomass necessary to support nesting insectivorous birds

B_3= carcass biomass necessary to support wintering bald eagles

B_n= carcass biomass necessary to support other parts of the ecosystem such as bears, mink, herptiles, waterfowl, other fish, plants, etc.

The biomass must then be converted to numbers of spawners so that individual runs of fish can be managed.

Carcass Biomass to Support Salmonid Smolts (B_1)

For ease of calculation, it was assumed that salmonid smolts only consumed invertebrates (mostly insects) in freshwater. In the Skagit River watershed, estimates are available for the smolt production for chinook and coho salmons and steelhead trout; all have extended rearing in the watershed. At present, estimates of the number of cutthroat trout and native char are not available. Inclusion of cutthroat and char would increase the estimate of carcass biomass necessary to support salmonid smolts. Estimates of smolt production for those species that make extensive use of the freshwater environment for rearing were developed from actual trapping data or calculations based on available habitat or average survivals. Tweit (WDFW biologist, pers. comm.) estimated that 4,296,000 chinook salmon smolts are produced under average environmental conditions when current escapement goal was met. Actual trapping on the Skagit River estimated that 1,100,000 coho salmon smolts are produced (D. Seiler, WDFW biologist, pers. comm.). This number is less than the smolt production potential of 1,453,878 estimated by Zillges (1977) and substantially less than the smolt production potential of 2,146,701 estimated by Johnson (1986) but represents the current situation in the watershed.

No estimates of actual smolt potential for steelhead trout in the Skagit system are available, so WDFW based the escapement goal on the number of parr (372,672) rearing in the stream during the summer before smolting (Northwest Indian Fisheries Commission et al. 1985). For each species, the biomass of smolts or parr was estimated by using 7g for chinook salmon, 14g for coho salmon and 20g for steelhead trout, which represented mean individual fish weights observed in western Washington (WDFW files). Assuming that the fish consume only insects, a conversion factor of 4.0 (Piper et al. 1986) was used to convert the smolt/parr biomass to the insect biomass required by the smolts or parr.

Carcass Biomass Needs for Nesting Insectivorous Birds (B_2)

In his discussion of the transport of marine nutrients to upland areas, Sibatani (1996) estimated that nesting birds in the Shiga Highlands, a conifer forest in Japan, consumed 10,000 kg of insects per km^2 of forest from May to October. This estimate was used to apply to the riparian forests of the Skagit River watershed because a local estimate could be located. Sibatani (1996) recognized that organic matter is lost through energy metabolism but that (pg. 7) " ... a cycle of inorganic elements whose weight is always conserved, there seems to be no problem in representing this weight with the live weight of insects and birds." Consequently, a direct conversion of carcass weight to insect weight was used to estimate the biomass of carcasses necessary to produce the insects for nesting birds. To apply this to the Skagit River watershed, a width of 100 m on each side of the stream in the anadromous zone (905.4 km) was assumed to be most directly affected by the carcasses and the 10,000 kg/km^2 was applied to that area.

Carcass Biomass for Overwintering Bald Eagles (B_3)

Stalmaster and Gessaman (1984) estimated that a bald eagle wintering along the Skagit River requires 486 g of salmon flesh per day. Hunt et al. (1992) estimated Skagit River wintering eagle populations from 1973-81. For the winter of 1980-81 they estimated 4,396 kg of salmon was necessary to support the eagles, but this eagle population (1980-81) was only 33.1% of the largest wintering

population estimated between 1973 and 1981. Supporting the largest population required 13,284 kg of carcasses.

Converting Biomass to Numbers of Fish in the Escapement Goal

Seiler (WDFW Biologist, pers. comm.) observed that in years when pink salmon spawn in the Skagit River, more than 1 million coho salmon smolts were produced the following spring, while in non-pink salmon spawning years, the average annual smolt production was 650,000 coho salmon. When coupled with Michael's (1996) study of interactions between pink salmon and coho salmon, and the fact that in Washington pink salmon essentially spawned only in the early fall of odd numbered years, and the only other early fall spawning salmon in the system was the chinook salmon, it is assumed that a similar biomass of carcasses was needed in the fall of even numbered years to obtain similar numbers of coho salmon smolts. From Seiler's data, an escapement of 500,000 pink salmon maximized the production of coho salmon smolts under current watershed conditions. Thus, 500,000 was used as the escapement goal for pink salmon. The biomass of 500,000 pink salmon spawners was divided by the mean weight of adult Skagit River chinook salmon to obtain a goal for non-pink years. In the current management scheme, spring chinook salmon comprise 16.8% of the total chinook salmon escapement goal with the remainder being a mixture of summer and fall chinook salmon. The relationship between the two groups of chinook salmon was maintained in the proposed goals.

Conceptually, it might appear appropriate to increase the chinook salmon escapement goal only in even numbered years because of pink salmon presence in odd numbered years. Having different escapement goals for even and odd years is used for chum salmon (*O. keta*). However, consumptive fisheries for chum salmon occur only on maturing fish, while consumptive fisheries for chinook salmon occur over most of the life cycle with a substantial portion of the marine harvest taken as immature fish. In order to have an even year and an odd year escapement goal for chinook salmon and still maintain marine fisheries on immature fish it will be necessary to have some sort of external mark which will identify at what age the fish will mature. This mark currently does not exist. It would be possible to use different escapement goals for chinook salmon if all fisheries were conducted in the river of origin on returning spawners.

Ames (1983), in a discussion of salmon stock interactions in Puget Sound, suggested that increases in total Puget Sound pink salmon spawning escapement would reduce recruit per spawner for Puget Sound chum salmon. He surmised that pink salmon fry would outcompete chum salmon fry for food. To maintain a balance within the Skagit River watershed, the escapement goals for chum salmon were increased by the same proportion as the increase in the pink salmon escapement goal. Chum salmon in Puget Sound show two distinct population sizes. The run sizes and escapement goals in even numbered years are substantially higher than in odd numbered years; this same relationship was maintained in the development of the proposed goals. For coho salmon, the smolt per adult spawner ratio of 15.2 observed over 14 years of trapping at Snow Creek (Johnson and Cooper 1993) was multiplied by the Skagit River coho salmon smolt estimate of 1,100,000 to calculate the required escapement.

Results

The Skagit River watershed, under average environmental conditions and current spawning escapement goals (as defined by WDFW), should require 200,000 kg of salmon carcasses to support smolt production, 13,000 kg of carcasses to support wintering bald eagles, and 1,800,000 kg of carcasses to support insectivorous bird nesting and brood rearing for a total requirement of 2,000,000 kg (Table 1). The spawning escapements in the Skagit River watershed during 1970-1994 were consistently lower than this (Table 2). Even if all salmon species met their present

TABLE 1. Biomass (kg) required for salmonid smolts produced, birds nesting within 100 m of streams, and for wintering bald eagles in the Skagit River watershed.

Consumer	Biomass
Salmonid smolts and parr	205,704
Riparian zone nesting birds	1,810,820
Overwintering bald eagles	13,284
Total	2,029,808

TABLE 2. Natural salmon escapement, in numbers and biomass, to the Skagit River, 1970-1994.

Species	Spawning escapement (N)			Biomass (kg)		
	Goal	Mean	Frequency of Goal Achievement	Maximum	Minimum	At Goal
Chinook						
Spring	3,000	1,509	0.040	26,830	6,149	29,283
Summer/Fall	14,900	12,861	0.320	242,609	57,746	145,439
Total	17,900	14,870	0.320	268,777	65,310	173,746
Coho	30,000	21,884	0.280	130,993	28,060	100,788
Pink	330,000	383,692	0.583	1,643,934	213,380	779,064
Chum						
Even year	117,800	107,407	0.538	931,233	115,528	679,211
Odd year	38,900	28,392	0.333	473,713	27,491	224,289
All species						
Even year						953,745
Odd year						1,277,887

escapement goal, only 45% to 60% of the required biomass (Tables 2 and 3) would be realized. Pink salmon and even-year spawning chum salmon show the best performance, having met or exceeded established goals slightly more than half the time.

To supply approximately 2 million kg of carcasses, salmon escapement goals for the watershed should be increased to 20,400 spring chinook salmon, 101,200 summer and fall chinook salmon, 72,400 coho salmon, 500,000 pink salmon, and 178,500 and 59,000 even and odd year chum salmon, respectively (Table 3). These goals represent substantial increases for chinook and coho salmon but represent levels of escapement occasionally met by chum salmon or regularly met by pink salmon in the Skagit River watershed.

TABLE 3. Proposed spawner escapement goals and potential biomass (kg) for Skagit River chinook salmon, coho salmon, pink salmon, and chum salmon.

Species	Spawning Escapement	
	Number	Biomass
Chinook		
Spring	20,400	198,012
Summer/Fall	101,200	982,296
Total	121,600	1,180,308
Coho	72,400	243,235
Pink	500,000	1,180,400
Chum		
Even year	178,500	1,029,195
Odd year	59,000	340,181
All Species		
Even year		2,452,738
Odd year		2,944,124

Discussion

The estimated biomass of carcasses required to meet wintering eagle, nesting bird, and salmonid smolt production in the Skagit River system is approximately twice the amount currently provided by the spawner escapement goals targeted in the present management scheme. Because the current management framework rarely achieves the escapement goal for any single species, and never achieved the escapement goal for all species in any year from 1970 to 1994, it can be assumed that the current management practices result in a deficit in the return of nutrients to the watershed. Further, because the estimate is a minimum requirement for only a fraction of the consumers of nutrients in the system, it is probable that the system as a whole has a severe nutrient deficit.

Nutrient deficit is probably a coastwide problem. The National Research Council (1996) estimated that 6 to 10% of the historic levels of salmon spawners and associated nutrients are returning to the Willapa Bay Basin, located in southwestern Washington. Historic spawning escapements and total run sizes were difficult to estimate because data is lacking or inconsistent. Most early (late 1800s through mid 1900s) fishery data only reported catch and rarely quantified escapement. Additionally, reports of run sizes (catch plus escapement) sometimes varied widely. For example,

Ricker (1987) and Gilhousen (1992) reviewed available data for Fraser River sockeye salmon (*O. nerka*) between 1890 and 1920; Ricker (1987) estimated the total run to be 100 million fish and Gilhousen estimated the run at 40 million fish. Prior to the development of commercial fisheries this number would have approximated the actual number of fish which entered the river to spawn or to be consumed by watershed residents such as bears, eagles, and humans. Between 1938 and 1993 the largest sockeye salmon spawning escapement was estimated at about 6.4 million (Roos 1991; Pacific Salmon Commission 1996). The percentage of current versus historic levels of escapement vary from a low of 6% to a high of 16%, which are similar to those estimated for Willapa Bay.

Are the proposed escapement goals reasonable and comparable to levels of escapement seen in other areas? As mentioned earlier, pink salmon and chum salmon escapements in the Skagit River watershed currently approach or exceed the proposed goals. Bilby (Weyerhaeuser biologist, pers. comm.), based on stable isotope analysis, believes that coho salmon escapement in small tributaries needs to be between 150 and 225 spawners/km. For the Skagit River watershed tributaries alone this would result in an escapement goal of between 46,000 and 69,000 coho salmon. While the proposed escapement goal for Skagit River chinook is substantially higher than has been managed for in the past, it does not represent a spawner escapement that is unheard of in other areas. The escapement goal is proposed to be 135 spawners/km of stream. The Pacific Fishery Management Council (1979) reported 213 chinook salmon per km as the 1970s' escapement level for the Sacramento River system with a goal of 286 spawners/km.

Can the present habitat in the Skagit River watershed support the proposed increases in spawning? The answer must be yes and no. The spawning and incubation environment currently supports chum salmon and pink salmon spawning at or above the proposed levels. However, one outcome of industrial logging and associated road building in a western Cascade mountain watershed in Oregon has been that peak flows have increased between 50 and 100% (Jones and Grant 1996). In addition to logging, the Skagit River watershed has roads, towns, housing developments, and other impervious surfaces which exacerbate runoff peaks. Recent data and observations suggest that streamflows during incubation are excessively high, leading to higher losses of eggs (D. Seiler, WDFW biologist, pers. comm.) than would occur under more moderate flows.

There is also evidence that streams may not be able to retain all of the carcasses due to man-made changes in the watershed. Recent studies have shown that habitat complexity, as measured by the amount of debris and rock in a channel, increases the ability of a stream to retain carcasses and cycle nutrients (Cederholm and Peterson 1985, Sedell et al. 1988, Dobson et al. 1992). Much of the land abutting reaches of the Skagit River watershed accessible to anadromous salmonids is managed for industrial logging which changes the riparian area, flow regimes, and amounts of large woody debris in streams. Growns and Davis (1991) showed that 8 years after logging, there were still significant differences in the aquatic invertebrate communities between clear-cut and unlogged areas. Changes in insect communities will probably be reflected in the way nutrients from the carcasses are captured and cycled within the stream. The lowland areas of the Skagit River watershed have been leveed, diked, and otherwise constrained so that the river channel serves more to conduct water through the area than to produce fish and other aquatic and riparian resources. The river also has a series of hydroelectric dams which have blocked some areas previously available for anadromous fish spawning and have changed the flow regimes due to water storage and electrical power generation. If the Skagit watershed's present ability to capture, retain, and cycle nutrients was less than in pre-development times it will either be necessary to further increase escapements in order to actually incorporate the nutrients into the system or make improvements to the habitat.

In theory, the escapement goals for the less economically valuable, but more abundant, chum salmon and pink salmon could be raised to meet the carcass biomass goals so that present fishing patterns on chinook salmon and coho salmon would not be disrupted. This would meet the calculated nutrient needs of wintering eagles, nesting birds, and salmonid smolt production, but, it does not consider the importance of spatial and temporal distribution of different salmonid species. As noted before, the difference in smolt production related to the presence or absence of pink salmon spawners means that the spatial and temporal overlap is as

critical as the number of biomass of carcasses. The only way to increase coho salmon smolt production in non-pink salmon spawning years is to increase the chinook spawning population which spawns at about the same time and often in the same areas, as the pink salmon. The timing of available carcasses was also critical to eagles. Hunt et al. (1992) demonstrated that Skagit River eagles fed first on chum salmon then on coho salmon carcasses when the chum salmon run was finished. They showed that the current fishery management plans do not provide enough coho salmon carcasses to meet the nutritional needs of eagles. Consequently, the eagles eventually left the area in search of other foods (Hunt et al. 1992).

The spatial distribution of carcasses through the watershed also needs consideration. Of the four salmon species under consideration, the chinook, pink, and chum salmons typically spawn in mainstems or in the lower reaches of tributaries. Coho salmon penetrate as far into a watershed as flows allow. In addition to the coho salmon carcasses delivering nutrients into headwater areas, there is some evidence (B. Bilby, Weyerhaeuser Biologist, pers. comm.) that steelhead trout juveniles follow the salmon upstream so that they can feed on the eggs and carcasses. This redistribution of juvenile steelhead trout puts them into an environment that was, from a historic and evolutionary perspective, more stable during winter. Consequently, increasing the number of coho salmon spawners should directly benefit the survival of steelhead trout. Dolly Varden and bull trout are regularly observed to be stationed downstream of spawning salmon, presumably to feed on eggs and insects disturbed by the spawners.

Once these goals are set can they be achieved? For pink salmon and chum salmon the answer is yes. Recent escapements for pink salmon have exceeded the proposed 500,000 spawners; continuation of current fishery patterns can achieve this escapement goal. For chum salmon, the run of fish entering Puget Sound is regularly greater than the proposed goal (WDFW files). Thus, fishery reductions could achieve the proposed escapement goal.

The situation for coho salmon and chinook salmon is more complex. In the 25 years examined, both species had total returns (catch plus escapement) to Skagit Bay that were almost always less than half of the proposed goals. These two species differ from the pink salmon and chum salmon in that an estimated 50-80% or more of the harvest occurs in fisheries outside of Puget Sound are, therefore, not controlled by Washington or tribal co-managers (Washington Dept. of Fisheries 1984). Increasing the escapement of these two species to the proposed levels will require many years in which fishing in Alaska, British Columbia, and coastal Washington will need to be constrained. Politically, this is unlikely unless there is a coast-wide recognition of the need to make similar increases in escapement throughout the species' ranges.

Salmon management, as with most other natural resource management, is imprecise. No estimate, such as run size, spawning escapement, or catch, is exact. In Washington, managers assume that errors are random and balance out over time. From this perspective, if the average spawning escapement for a species is met, then management intent has been achieved. If managers intend to annually achieve or exceed a precise escapement goal, annual fishery priorities will need revisiting.

The benefits of increased carcass deposition will accrue over time. The increased availability of carcasses will quickly translate into more and larger juvenile fish (Bilby, Weyerhaeuser biologist, pers. comm.), which should help improve their marine survival (Holtby et al. 1990). Increases in bird populations may take longer; studies where a segment of forest was fertilized showed increases in populations three years after the project began (Folkard and Smith 1995). Hunt et al. (1992) showed that the number of bald eagles wintering on the Skagit River was directly related to the magnitude of chum salmon escapement and carcass availability. Increased numbers of carcasses should increase the wintering populations. The impact of increased winter food supply on the reproductive success of eagles will need to be determined through further studies.

The increased number of spawners should also change the hydrology of the system. Montgomery et al. (1996) showed that mass spawning by salmon actually changes stream bottom composition and configuration so that a higher flow is needed to begin to scour the bed than in a stream with fewer spawners. Increased resistance to scouring should improve survival for eggs incubating in the streambed. In addition, the act of digging a redd for spawning resuspends fine sediments which

are transported downstream and out of the spawning grounds.

There is a limit to the number of spawners a stream can accommodate. Since Euro-American settlement of the Skagit River watershed, a number of changes have permanently reduced the spawning area available to adult salmonids (Sedell et al. 1988, Palmisano et al. 1993, McIntosh et al. 1994, Wissmar et al. 1994). These modifications include dredging, log jam removal, dam construction, water removal for municipal and industrial use, draining and filling sloughs, and so on. The proposed goals may provide for more adults than will be able to successfully spawn in the river. However, a single large escapement which does not produce at least an equivalent number of returning adults does not necessarily indicate that excessive spawning occurred. Outside forces and catastrophic events such as floods, droughts, or ocean conditions also affect spawning in a given year. A good model for rebuilding salmon populations is the one used for Fraser River sockeye salmon. There, escapement goals were considered experimental and increased incrementally as data on total run, adult returns, spawner distribution, and spawner success, became available (Roos 1991).

The proposed escapement goals are based on the current understanding of the system and will change as spawner levels rise. For example, the chinook salmon smolt numbers are based on the smolt production by the current goal of 17,900 spawners. An escapement of 121,600 should produce substantially more smolts; their food requirements are not included in developing the goal of 121, 600. The coho salmon goal uses the number of smolts currently being trapped in the watershed. Johnson (1986) estimated that the watershed could produce about twice as many smolts. As with chinook salmon, increases in the number of coho salmon smolts were not included in the development of these goals. Hunt et al. (1992) showed that eagles follow food resources; thus more salmon on the Skagit River will attract more eagles. When the number of eagles wintering on the Skagit River exceeds the number from the winter of 1978-79, their nutritional needs will need to be factored in. Lastly, there are several different methods for estimating the energy and nutritional requirements for each group of consumers. Sibatani (1996) was using an estimate that presumed that mass was conserved; it would take 1 kg of carcass flesh to produce 1 kg of insect flesh. Piper et al. (1986) included energy transfer and waste products in their calculations of the amount of insect flesh needed to produce 1 kg of fish flesh. Hunt et al. (1992) and Stalmaster and Gessaman (1984) estimated bald eagle food needs based on observations of eagles consuming salmon during the winter. Sibatani's (1996) estimate is probably the most conservative because it assumes perfect transfer of nutrient mass. The other two estimates are probably closer to the actual nutrition need because they are based on observations of actual consumption.

The proposed escapement goals are point estimates and it is recommended that they be treated as fixed points rather than developing a range of escapements from which managers can choose. Conceptually, a range of goals offers the manager flexibility to balance available fish with the desire to harvest. Further, a range recognizes that the actual ecosystem need will, in fact, vary over time as conditions change since nature is not stable. The reality is that salmon management is imprecise and the use of a fixed point goal still results in a range of escapements (see Table 2). Anyone familiar with salmon management on the Pacific coast of North America knows that fisheries are driven by harvest. Annually, some runs are deliberately overfished in order to allow for the harvest of commingled abundant stocks. If a range of escapement goals were adopted the result would be to consistently fish to the lower end of the range. The result will be to perpetuate the current nutrient deficit.

There is at least one more question which needs to be debated. If the Pacific Northwest ecosystems evolved to process returning anadromous fish, then how many fish can be removed from the system without reducing the ecosystem's productive capacity? Before the development of canneries and product distribution systems, the carcasses generally stayed in the watershed even if they were consumed by terrestrial animals and humans. If this is how a watershed ecosystem evolved, and if the same level of terrestrial and aquatic consumers can still exist in the system, then harvests which remove the carcasses from the watershed may need to be kept much lower than today's levels of overall exploitation. There needs to be serious consideration, study, and public debate of the idea that naturally spawned populations of anadromous salmonids belong in the

river. Consumptive harvests, particularly outside of the river of origin, may need to come from captive raised fish or through the selective harvest of ocean ranched fish.

Summary

A new method to develop spawner escapement goals for Pacific salmon was developed using the Skagit River watershed as an example. These goals were based on the premise that Pacific Northwest watersheds derived most of their nutrients from the annual spawning migrations and death of the salmon. Based on estimates of carcass biomass necessary to support breeding riparian zone bird populations, wintering bald eagles, and the production of stream-rearing salmonid smolts, the methodology results in recommendations that 20,400 spring chinook salmon, 101,200 summer/fall chinook salmon, 74,400 coho salmon, 500,000 pink salmon, and 178,500 and 59,000 even and odd year chum salmon be allowed to spawn. These goals should be relatively easy to achieve for the pink and chum salmons but will be more difficult to achieve for chinook and coho salmons because of the multi-jurisdictional nature of the consumptive fisheries applied to them. Further, it will be critical to ensure, through habitat restoration and protection programs, that the watershed is capable of retaining and cycling the nutrients delivered by the carcasses. The results of this study suggest that Pacific Rim watersheds need substantially more salmonid spawners than current management regimes allow. How the current level of consumption of these fish is maintained will need serious debate.

Acknowledgements

I wish to thank R. Bilby, P. Bisson, S. Evans, and R. Fuller for their comments, suggestions, discussion, and encouragement in developing the concepts for this paper. K. Buchanan, R. Glesne, D. Hendrick, P. Michael, J. Tipping, G. Vander Haegen, and an anonymous reviewer provided critical review and suggestions which substantially improved the manuscript.

Literature Cited

Ames, J. J. 1983. Salmon stock interactions in Puget Sound: a preliminary look. *In* M. A. Miller. Southeast Alaska coho salmon research and management review and planning workshop. Alas. Dept. Fish and Game Rep., Juneau, Alaska. Pp.84-95.

Ben-David, M., T. A. Hanley, D. R. Klein, and D. M. Schell. 1997. Seasonal changes in coastal and riverine mink: the role of spawning Pacific salmon. Can. J. Zool. 75:803-811.

Bilby, R. E., B. R. Fransen, and P. A. Bisson. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. Can. J. Fish Aquat. Sci. 53:164-173.

Cederholm, C. J., D. B. Houston, D. L. Cole, and W. J. Scarlet. 1989. Fate of coho salmon (*Oncorhynchus kisutch*) carcasses in spawning streams. Can. J. Fish. Aquat. Sci.46:1347-1355.

Cederholm, C. J. and N. P. Peterson. 1985. The retention of coho salmon (*Oncorhynchus kisutch*) carcasses by organic debris in small streams. Can. J. Fish. Aquat. Sci. 42:1222-1225.

Dobson, M., A. G. Hildrew, A. Ibbotson, and J. Garthwaite. 1992. Enhancing litter retention in streams: do altered hydraulics and habitat confound field experiments? Freshwater Biology 28:71-79.

Folkard, N. F. G. and J. N. M. Smith. 1995. Evidence for bottom-up effects in the boreal forest: Do passerine birds respond to large-scale experimental fertilization? Can. J. Zool. 73:2231-2237.

Gilhousen, P. 1992. Estimation of Fraser River sockeye escapements from commercial harvest data, 1892-1944. Internat. Pac. Salm. Fish. Comm. Bull XXVII. Vancouver. B.C. 114 p.

Growns, I. O. and J. A. Davis. 1991 . Comparison of the macroinvertebrate communities in streams in logged and undisturbed catchments 8 years after harvesting. Aust. J. Mar. Freshwater Res. 42:689-706.

Hilderbrand, G. V., S. D. Farley, C. T. Robbins, T. A. Hanley, K. Titus, and C. Servheen. 1996. Use of stable isotopes to determine diets of living and extinct bears. Can. J. Zool. 74:2080-2088.

Holtby, L. B., B. C. Anderson, and R. K. Kadowaki. 1990. Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. 47:2181-2194.

Hunt, W. G., B. S. Johnson, and R. E. Jackman. 1992. Carrying capacity for bald eagles wintering along a northwestern river. Raptor Res. Jour. 26:49-60.

Johnson, R. 1986. Assessment of the Skagit River system's coho rearing potential. WDF Tech. Rep. 96. Olympia, Washington 22 p.

Johnson, T. H. and R. Cooper. 1993. Anadromous game fish research annual performance report#93-23. Wa. Dept. Wild. Olympia, Washington 21 p.

Johnston, N. T., C. J. Perrin, P. A. Slaney, and B. R. Ward. 1990. Increased juvenile salmonid growth by whole-river fertilization. Can. J. Fish. Aquat. Sci. 47:862-872.

Jones, J. A. and G. E. Grant. 1996. Peak flow responses to clear-cutting and roads in small and large basins, western cascades, Oregon. Water Res. Res. 32:959-974.

Kline, T. C., Jr., J. J. Goering, O. A. Mathisen, P. H. Poe, and P. L. Parker. 1990. Recycling of elements upstream by runs of Pacific salmon: I. ^{15}N and ^{13}C evidence in Sashin Creek, southeastern Alaska. Can. J. Fish Aquat. Sci. 47:136-144.

Kline, T. C., Jr., J. J. Goering, O. A. Mathisen, P. H. Poe, P. L. Parker, and R. S. Scalan. 1993. Recycling of elements upstream by runs of Pacific salmon: II. ^{15}N and ^{13}C evidence in the Kvichak River watershed, Bristol Bay, southwestern Alaska. Can. J. Fish Aquat. Sci.50:2350-2365.

Koenings, J. P. and R. D. Burkett. 1987. An aquatic Rubik's cube: restoration of the Karluk Lake sockeye salmon (*Oncorhynchus nerka*). *In* H. D. Smith, L. Margolis, and C. C. Wood (ed.), Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Pub. Fish. Aquat. Sci.96. Pp. 419-434.

Kyle, G. B. 1994. Assessment of trophic-level responses and coho salmon (*Oncorhynchus kisutch*) production following nutrient treatment (1981-1986) of Bear Lake. Alaska. Fish. Res. 20:243-261.

Larkin, G. A. and P. A. Slaney. 1997. Implications of trends in marine-derived nutrient influx to south coastal British Columbia salmonid production. Fisheries 22:16-24.

McIntosh, B. A., J. R. Sedell, J. E. Smith, R. C. Wissmar, S. E. Clarke, G. H. Reeves, and L. A. Brown. 1994. Historical changes in fish habitat for select river basins of eastern Oregon and Washington. NW Sci. 68:36-53.

Michael, J. H. Jr. 1995. Enhancement effects of spawning pink salmon on stream rearing juvenile coho salmon: managing one resource to benefit another. NW Sci. 69:228-233.

Montgomery, D. R., J. M. Buffington, N. P. Peterson, D. Shuett-Hames, and T. P. Quinn. 1996. Stream-bed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. Can. J. Fish. Aquat. Sci. 53:1061-1070.

National Research Council. 1996. Upstream: salmon and society in the Pacific Northwest. Nat. Acad.. Press, Washington DC. 452 Pages.

Nehlsen, W., J. E. Williams, and J. A. Lecithic. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries 16:4-21.

Northwest Indian Fisheries Commission, Washington Department of Game, and *U.S. v. Washington* Case Area Treaty Tribes. 1985. Multiple river spawner-recruit functions for steelhead that incorporate an index of habitat. Joint Comm. Tech. Rep., Olympia, Washington. 22 p.

Pacific Fishery Management Council. 1979. Freshwater habitat, salmon produced, and escapements for natural spawning along the Pacific Coast of the U.S. Pac. Fish. Mgmt. Council. Portland, Oregon. 68 p.

Received 9 April 1998
Accepted for publication 3 September 1998

Pacific Salmon Commission. 1996. Report of the Fraser River Panel to the Pacific Salmon Commission on the 1993 Fraser River sockeye and pink salmon fishing season. Pac. Salm. Comm. Vancouver, BC. 58 p.

Palmisano, J. F., R. H. Ellis, and V. W. Kaczynski. 1993. The impact of environmental and management factors on Washington's anadromous salmon and trout, summary and recommendations. Wash. For. Prot. Assoc. and Wash. Dept. Nat. Res. Olympia, Washington. 54 p.

Piper, R. G., I. B. McElwain, L. E. Orme, J. P. McCraren, L. G. Fowler, and J. R. Leonard. 1986. Fish hatchery management. USDI, Washington, DC. 517 p.

Ricker, W. E. 1987. Effects of the fishery and of obstacles to migration on the abundance of Fraser River sockeye salmon (*Oncorhynchus nerka*). Can. Tech. Rep. Fish. Aquat. Sci. No. 1522. 75 p.

Roos, J. F. 1991. Restoring Fraser River salmon. Pac. Salm. Comm., Vancouver, B.C. 447 Pages.

Sedell, J. R., P. A. Bisson, F. J. Swanson, and S. V. Gregory. 1988. What we know about large trees that fall into streams and rivers. *In* C. Maser, R. F. Tarrant, J. M. Trappe, and J. F. Franklin (eds.) From the forest to the sea: A story of fallen trees. U.S. Dept. Agr. Gen. Tech. Rep. PNW-GTR-229., Portland, Oregon Pp. 47-81.

Sibatani, A. 1996. Why do salmon ascend rivers? Sel. Papers on Entropy Studies. 3:3-12.

Stalmaster, M. V and J. A. Gessaman. 1984. Ecological energetics and foraging behavior of overwintering bald Eagles. Ecol. Mono. 54:407-428.

Stalmaster, M. V. and J. L. Kaiser. 1997. Winter ecology of bald eagles in the Nisqually River drainage, Washington. NW Sci.71:214-223.

Stockner, J. G. and E. R. MacIsaac. 1996. British Columbia lake enrichment programme: two decades of habitat enhancement for sockeye salmon. Reg. Riv. Res. Mgmt. 12:547-561.

Washington Department of Fisheries. 1984. Strategic plan for managing Washington salmon stocks, Washington salmon stock inventory, appendices G-I. Wash. Dept. Fish. Olympia, Washington.435 pages.

Willson, M. F. and K.C. Halupka. 1995. Anadromous fish as keystone species in vertebrate communities. Cons. Biol. 9:489-497.

Wissmar, R. C., J. E. Smith, B. A. McIntosh, H. W. Li, G. H. Reeves, and J. R. Sedell. 1994. A history of resource use and disturbance in riverine basins of western Oregon and Washington (early 1800s-1990s). NW Sci. 68:1-35.

Wright, S. 1981. Contemporary Pacific salmon fisheries management. *In* R. Winget (ed.) Integration, Promises and problems in the Northwest seafood industry. Small Tribes Organ. West. Wa., Sumner, Washington. Pp. 46-55.

Zillges, G. 1977. Methodology for determining Puget Sound coho escapement goals, escapement estimates, 1977 pre-season run size prediction and in-season run assessment. Wash. Dept Fish. Tech. Rep 28. Olympia, Washington. 65 p.

Mason D. Bryant and **Fred H. Everest,** Aquatic/Land Interactions Research Program, Pacific Northwest Research Station, U.S.D.A. Forest Service, 2770 Sherwood Ln., 2A, Juneau, Alaska 99801

Management and Condition of Watersheds in Southeast Alaska: The Persistence of Anadromous Salmon

Abstract

In contrast to most of North America and Europe, numerous intact or lightly disturbed watersheds are present throughout southeast Alaska. These watersheds support abundant and diverse populations of anadromous salmonids. While the watersheds throughout the northern hemisphere have been exposed to human disturbance from millennia to centuries, significant human disturbance to the watersheds of southeast Alaska did not begin until the 1950's with the start of industrial logging. Although management of watersheds has evolved to reduce risks to aquatic habitat, the most intensive logging occurred during the first 20 years of timber harvest when few restraints were placed on timber harvest in watersheds. As a result, a legacy of streams with deteriorating habitat remains. While few salmon stocks in southeast Alaska appear to be in decline, escapement records on specific watersheds, particularly those most severely affected by management are non-existent or qualitative. The present status of salmon stocks may be attributed to abundant intact watersheds, high marine survival, and escapement levels that fully seed most watersheds. The numerous intact watersheds throughout southeast Alaska are a critical factor in maintaining sustainable salmon stocks in southeast Alaska.

Introduction

Hundreds of large and small, and mostly pristine watersheds are dispersed through the islands of the Alexander Archipelago of southeast Alaska. These watersheds are located in a small percent of the remaining temperate rain forests in the world that have not been moderately or severely altered by human activity. Furthermore, these watersheds support a disproportionately high proportion of the wild anadromous salmonid stocks remaining in the Pacific Northwest. Throughout the western United States and British Columbia, Canada, numerous stocks of anadromous salmonids are at risk of extinction, declining, or of serious concern to resource managers and users (Nehlsen et al. 1991; Slaney et al. 1996). Southeast Alaska is an exception with few stocks that have been identified in decline (Baker et al. 1996; Halupka et al. in press). This can be attributed largely to the absence of dams, agricultural and urban development, and intact watersheds in southeast Alaska. Intensive human exploitation of watersheds in southeast Alaska began only a few decades ago and is likely to continue as demand for resources grows with increasing human populations. The most significant potential risks to salmonid stocks in southeast Alaska include large scale habitat degradation and fishing pressure (Baker et al. 1996; Halupka et al. in press).

The purpose of this paper is to examine historical timber harvest patterns, management history, distribution of managed and intact watersheds, and their relationship to anadromous salmonid populations in southeast Alaska. The focus is on land managed by the U. S. Forest Service, the Tongass National Forest (TNF). Although the area of the Tongass National Forest is large, a relatively small portion is suitable for timber production and this portion often coincides with highly productive fish habitat. We briefly describe the development of "Best Management Practices" implemented by the U.S. Forest Service from the 1950s through 1996 and their application in watersheds in southeast Alaska. We examine timber harvest patterns to show the extent of disturbance in managed watersheds and how these patterns have changed from the start of industrial timber harvest to the present. We hypothesize that improvements in forest management practices within the past 5 years and retention of intact watersheds will be an important factor in maintaining healthy anadromous salmon populations in southeast Alaska.

The TNF is part of the temperate rain forest biome (Alaback 1991). Globally, the temperate rain forest consists of about 34.4 million ha (90 million acres) which includes parts of North America, Chile, New Zealand, Tasmania, and the former Soviet Union (Hagenstein 1993; TLMP

© 1998 by the Northwest Scientific Association. All rights reserved.

Revision 1997). About 50% of this biome occurs in North America with most located along the coasts of British Columbia and southeast Alaska (Ecotrust et al. 1995). About 14% (5.1 million ha) occurs in the TNF. About 2.0 million ha of the TNF is classified as old-growth forests and is commercial forest[1]. The remaining area consists of alpine, ice fields, muskegs, and areas with less than 10% tree cover. More than 70% of the commercial forest is below 492 m (1500 ft) elevation and of that more than 40% is below 262.5 m (800 ft) elevation (Figure 1). The area less than 262.5 m (800 ft) includes 1,450,000 ha of commercial and non-commercial forests and comprises the most productive valley bottoms. Of this, about 263,000 ha are riparian corridors (TLMP Revision 1997).

[1]commercial forest defined as having >8,000 board feet (b.f.) per acre.

Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) are the dominant trees at the lower elevations and in the stream valley bottoms (Viereck and Little 1972). These were the only economically valuable tree species until five years ago when yellow cedar (*Chamaecyparis nootkatensis*) also became economically important. Alaska yellow cedar extends throughout coastal south central Alaska, southeast Alaska, and southward through British Columbia (Viereck and Little 1972). Western redcedar (*Thuja plicata*) occurs in the southern portion of southeast Alaska. Mountain hemlock (*Tsuga mertensiana*) is found at higher elevations. Red Alder (*Alnus rubra*) is common along disturbed sites, either natural or anthropogenic, such as landslides, abandoned roads, and gravel bars along riparian areas. Understory of old-growth forests is generally comprised of younger trees and various shrubs and

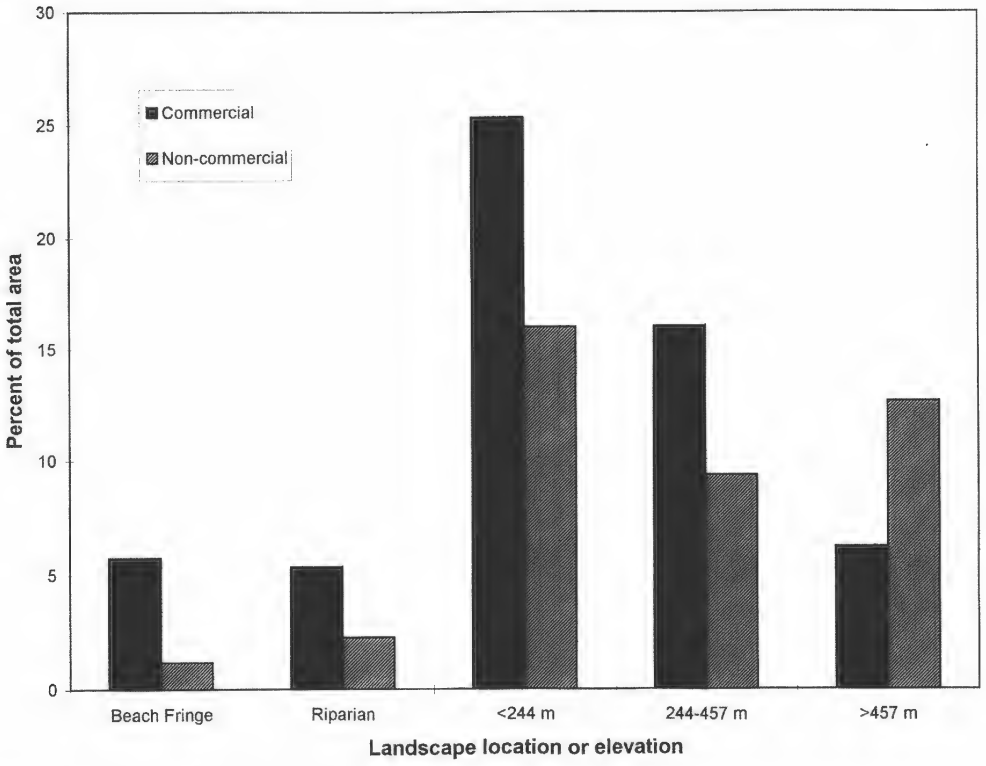


Figure 1. Distribution (% of area) of old-growth forest in southeast Alaska classified into commercial and non-commercial forest by landscape and elevation (TLMP 1997).

herbs including blueberry (*Vaccinium* spp), fool's huckleberry (*Menziesia ferruginea*), stink current (*Ribes bracteosum*), and devils club (*Oplopanax horridus*). A complete description of the vegetation is provided by Alaback (1980).

The landscape of southeast Alaska is geologically young. Most areas were glaciated during the late-Wisconsin glaciation which ended about 10,000 yr BP (Heusser 1960; Pewe 1975; Pielou 1992). The terrain is mountainous and characterized by steep-sided mountains and U-shaped valleys sculpted by glaciers (Harris et al. 1974). High rainfall and heavy snowpack at higher elevations (>300 m) combined with the steep topography drive a complex hydrological cycle that creates fall floods and high water in the spring as the snow melts (Schmiege et al. 1974). The steep, irregular topography and high precipitation contribute to a pattern of frequent natural disturbance events that include landslides and blowdown of large old-growth trees. The combination of varying flows, natural disturbance, and large old-growth trees creates complex stream ecosystems that support large and diverse communities of anadromous salmonids. These, in turn, support valuable commercial, sport, and subsistence fisheries for pink (*Oncorhynchus gorbuscha*), coho, (*O. kisutch*), sockeye, (*O. nerka*), chum (*O. keta*), and chinook salmon (*O. tshawytscha*) (Meehan 1974). The large salmon runs are a significant resource to terrestrial mammals and birds (Shochat 1993; Willson and Halupka 1995) as well as an important nutrient source for aquatic organisms (Cederholm et al.1989; Wipfli in press).

Historical Perspective of Watershed Disturbance

Rivers and their watersheds have been focal points for human occupation and large scale anthropogenic modifications and disturbances have occurred for millennia. Zuaderer (1985) documents the development of canals and irrigation systems of the Tigres and Euphrates river systems to support agriculture for the ancient city states of Ninevah and the Assyrian empire about 3000 yr BP. Watershed and riparian development throughout Europe began centuries ago, beginning with deforestation, agriculture, and more recently, industrial development (Petts 1989; Petts et al. 1989). As a result, few unmodified reaches remain. Atlantic salmon (*Salmo salar*) have been extirpated from many of the rivers. Remaining populations are maintained by hatcheries in numerous rivers throughout western Europe (Mills 1991).

Widespread exploitation of watersheds in North America has spanned three centuries beginning on the Atlantic coast with permanent European settlements in the early 1700's. River valleys were cleared for agricultural development, and streams and rivers were dammed for water power and small mills. Along the east coast of the United States, New England, in particular, loss of Atlantic salmon populations occurred more than 100 years ago and was largely unrecorded. Dams throughout New England extirpated natural runs of Atlantic Salmon throughout the region (Stolte 1981). Wissmar et al. (1994) reviewed chronology of disturbance on the watersheds of the Pacific Northwest which began with the fur trade in 1811. The following decades brought the development of mining, early settlement for agriculture, and livestock grazing throughout the Pacific Northwest. During the course of three centuries of watershed development in North America, no major watershed remains completely free of extensive human disturbance in the contiguous United States. By 1990, less than 20% of the old-growth forests remained in the Pacific Northwest, virtually all on public land (Lehmkuhl and Ruggiero 1991).

The literature reviewed by Wissmar et al. (1994) and McIntosh et al. (1994) suggested that most of the adverse effects of the development and exploitation of the watersheds in Pacific Northwest were largely unreported until the 1970's. They cited only three pre-1940 reports on habitat condition of these watersheds. During the 1980's, reports on the condition of habitat and salmon stocks appeared in greater numbers and by the 1990's several comprehensive reports on habitat condition revealed that large scale deterioration of habitat in the Columbia River basin occurred during the past century (cited in Wissmar et al.1994). The cumulative effects of habitat degradation, combined with over-exploitation, and declining ocean productivity for these stocks has placed 214 native, naturally spawning stocks of salmonids in Washington, Oregon, and California at varying degrees of risk of extinction (Nehlsen et al. 1991; FEMAT 1993). The list includes chinook, coho, sockeye, chum, and pink salmon, as well as steelhead (*O. mykiss*) and sea-run cutthroat trout (*O. clarki*). The combined effects of these factors has created the "salmon crisis" in the last decade. The degree of effect seems to be

related to the duration and density of human occupation.

Large scale anthropogenic influence on southeast Alaska watersheds is a relatively recent phenomenon. Even though European exploration of southeast Alaska began in the 1700's, it was primarily related to the development of the fur trade—sea otter and seals— and whaling and effects on the landscape were localized and relatively minor (McDougall 1993). Even after the purchase of Alaska in 1867 by the United States, timber harvest was restricted to easily accessible areas near the shoreline. By 1900, 14 sawmills were operating and harvested 8.45 million board feet. From 1910 to 1920, another 410 million board feet were harvested (Harris and Farr 1974). Sporadic timber harvest continued through 1950. Large scale harvest did not begin until after a 50-year timber contract for 8.25 billion board feet of timber was awarded to the Ketchikan Pulp Company in 1951 by the U.S.D.A. Forest Service (Harris and Farr 1974). In 1956, a second 50-year timber contract for 5.31 billion board feet of timber was awarded to the Alaska Lumber and Pulp Company. Timber harvest for the two 50-year contracts marks the beginning of industrial forestry and major watershed disturbance in southeast Alaska.

From 1950 through 1992, more than 14 billion board feet of timber were removed from the Tongass National Forest (Murray 1970; Ruderman 1985; Warren 1996). From 1980 through 1994, about 5.9 billion board feet were harvested from private land in Alaska, most of which occurred in southeast Alaska (Ruderman 1985; Warren 1996). The peak harvest on the TNF occurred during the late 1960's through the early 1970's (Figure 2). From 1982 through 1986 harvest was about 1.4 billion board feet. As National Forest land was transferred to private ownership, timber harvest on private lands exceeded that on the TNF. The combined harvest from the TNF and from private

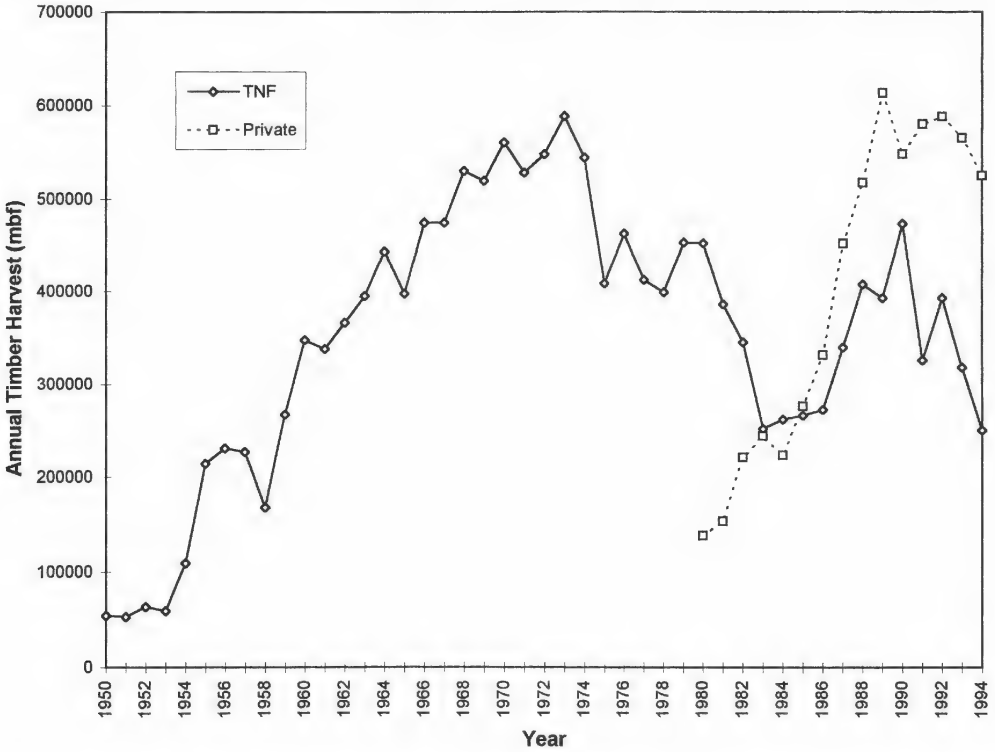


Figure 2. Annual timber harvest in southeast Alaska from the Tongass National Forest (TNF), and state and private lands from 1950 through 1994.

land from 1988 to 1994 was greater than the highest harvest on TNF lands at any point. The mill in Sitka closed in 1994 and a decline in timber harvest occurred on the TNF. The pulp mill in Ketchikan closed in 1997 further decreasing the demand for timber from the TNF.

History of Management Practices in Southeast Alaska

We separate management of riparian areas and stream habitat in the TNF into five intervals: 1950 to 1970; 1971 to 1982; 1983 to 1990; 1991 to 1996; and from 1997. The last period began with the adoption of the Tongass Land Management Plan (TLMP) by the U.S. Forest Service in May 1997. The intervals do not represent precise changes in management policies with the exception of 1991 when buffer strips 32.5m (100 ft) along fish streams were mandated (TTRA 1990). Changes throughout other periods were less apparent in administrative documentation, but the degree of protection to aquatic resources during timber harvest increased during each time interval.

1950-1970

From 1950 to 1970, logging generally proceeded up an entire stream basin with clear-cut logging from the streambank up to an elevation of about 324 m (800 ft). Although felling timber into streams and yarding across streams was prohibited, this was not strictly enforced. Trees were felled into creeks and removed during logging.[2] Logs were often dragged across streams or in some cases logs were dragged along streams. Tractor logging was often used in low gradient riparian areas and road crossings were made through streams. Heavy equipment was operated in streams and along stream banks. Log jams (large woody debris), both natural or resulting from logging operations, were systematically removed from streams either because they were perceived as blocks to migration or created pools that removed spawning areas. Evaluation of the effects of logging was generally accomplished by site inspections which frequently reported equivocal effects.[2] For example, "The tractor road channel may or may not be detrimental." Few guidelines for road layout or design that addressed the protection of aquatic habitat were available (U.S.D.A. Forest Service 1960).

[2]unpublished report. The effect of logging on twelve salmon streams in southeast Alaska. On file with the primary author.

1970-1982

The Logging and Fish Habitat Pamphlet of 1976 outlined improved forest practices for fish streams (U.S.D.A. Forest Service 1976). It identified the significance of small tributaries to juvenile salmonids, steelhead, and non-anadromous species such as Dolly Varden (*Salvelinus malma*) and cutthroat trout. Although the pamphlet recognized the importance of woody debris as cover for fish and cautioned against over-zealous debris removal, it did not recognize the significance of large wood on stream morphology and suggested that large accumulations were blocks to migration and affected spawning habitat. Extensive stream cleaning continued unabated from 1971 through 1982 (Bryant 1983). Examples of road construction, bridge and culvert crossing design, and construction timing to minimize the effect of sediment in streams were given in the Logging and Fish Habitat Pamphlet (U.S.D.A. Forest Service 1976). Significant improvements in aquatic habitat protection were implemented during this period in comparison to the previous 20 years, but streams in most watersheds that were logged during this period had no buffer strips and removal of large wood from most main stem and tributary streams was a common practice. Culverts were often installed that were too small for frequent floods in autumn and washed out. Others were improperly installed and were blocks to adult and juvenile salmonid movement (Bryant personal observation).

1983-1990

The 1979 Tongass Land Management Plan (TLMP 1979), the Alaska Regional Guide (U.S.D.A. Forest Service 1983), and a 1984 review of the Plan (U.S.D.A. Forest Service 1984) incorporated extensive sets of recommendations for stream habitat protection. The Plan in 1979 classified streams with anadromous fish as class I; streams with non-anadromous fish as class II; and tributaries or upstream sections of streams without fish that flow into fish bearing streams as class III. Each stream class was given a different level of protection with the highest afforded to class I streams. Riparian vegetation was retained to provide shade for temperature sensitive streams. Small tributary streams were recognized as habitat for resident trout and Dolly Varden. Riparian habitat was managed to provide large wood to streams that were identified as rearing habitat for identified

species. The recommendation for these streams was to retain all trees that were along the streambank and less than 30.5 cm in diameter at about 1.5 m above ground. Directional felling away from the stream channel was required as was full suspension of timber over streams (i.e. logs were completely elevated above the ground) during yarding operations. Logging in the riparian zone continued as a common practice. Where buffer strips were left, they were generally no wider than one tree height and usually were smaller, non-merchantable trees. In some cases, old-growth buffer strips were left along low gradient floodplain areas such as sections in the upper section of the South Fork of Staney Creek on Prince of Wales Island.

Retention of large wood in streams was included as a management practice in the 1986 Aquatic Habitat Management Handbook as a result of literature demonstrating the importance of large wood in the streams of the Pacific Northwest and Alaska (Swanson et al. 1976; Keller and Talley 1979; Bryant 1983; and Dolloff 1983 among others). Removal of woody debris was restricted to logging slash less than 4 cm diameter, although logging slash was to be prevented from entering the stream in the first place. The handbook specifically recommended against "removal of small debris jams in rearing streams". The large scale removal of woody debris prevalent before 1983 was largely discontinued throughout southeast Alaska (Bryant personal observation).

Significant improvements and specific recommendations for road layout, construction, and stream crossings were included in the Aquatic Habitat Management Handbook (U.S. Department of Agriculture 1986). Practices were incorporated to provide fish passage for both adult and juvenile salmonids and to minimize sediment production. These recommendations included information from an increasing number of reports on methods for forest road construction and stream crossing (Dane 1978; Anderson and Bryant 1980). Although the improved practices were applied and served to reduce effects of roads and stream crossing structures on aquatic habitat, implementation or effectiveness was not systematically monitored and numerous instances where procedures were either not followed or improperly applied occurred throughout the region. More significantly as roads were closed, many stream crossing structures were either not removed or improperly removed. As a result long term, chronic erosion and sediment transport sources were created.

1991-1996

The most obvious change in management in 1991 was the requirement for buffer strips that were at least 32.8 m (100 ft) wide where no trees would be cut along class I, and II streams that flowed into anadromous fish streams (Tongass Timber Reform Act 1990). It included provisions of the Aquatic Management Handbook (U.S. Department of Agriculture 1986). The "Best Management Practices" in the Soil and Water Conservation handbook (U.S. Department of the Agriculture 1993) were applied to protect riparian habitat and stream habitat in managed watersheds. Some significant additions in the Soil and Conservation Handbook were the recognition of riparian areas and floodplains, and specification of management practices to protect habitat beyond the mandated 32.8 m buffer zone. It states that "preferential consideration to riparian dependent resources will be given when conflicts among land use activities occur". The handbook also presents monitoring as an "essential" part of "Best Management Practices" and describes procedures and three stages of monitoring to evaluate management practices. Specific prescriptions are given to maintain channel integrity of all streams including non-fish streams. Guidelines are provided to reduce the potential for mass failures from road construction and location, road crossings, and log decks.

The set of management practices used from 1990 through 1996 were a significant improvement from those in place at the onset of industrial timber harvest and represented an accumulation of management and research information during that period. Throughout the evolution of "Best Management Practices" implementation was unevenly applied. In the absence of effective monitoring, detrimental streamside harvest practices such as debris removal, improper road and culvert installation and maintenance continued even after they were identified in various administrative directives. To the benefit of some watersheds, management practices exceeded those required by various directives. In many watersheds, buffer strips were extended beyond 32.8 m, particularly in floodplains. While the practices

used from 1991 through 1996 generally provided good protection to streams used by anadromous and non-anadromous salmonids, they did not address many of the important intermittent and higher gradient streams that are an integral part of the drainage systems in watersheds. Most of these systems are at elevations above 262.5 m (800 ft) and may not support perennial fish populations. However, they can have a significant influence on downstream habitat and fish populations (Heede 1972; Benda 1990; and Lamberti et al. 1991).

In 1994, the U.S. Congress directed the USDA Forest Service to review existing habitat protection for salmonid streams on the Tongass National Forest to determine their effectiveness (U.S. Department of Agriculture 1995). The report included an extensive literature review on Pacific salmon and their habitat in southeast Alaska and the Pacific Northwest, examined existing data and information on salmonid populations and their habitat in the Tongass National Forest, and reported results from a field evaluation of seven watersheds by a staff of Federal fisheries and watershed professionals (U.S. Department of Agriculture 1995). The assessment also included a pilot watershed analysis of three watersheds in southern, central, and northern southeast Alaska. Some of the key recommendations in the report were for increased protection of headwater streams, ephemeral streams, and non-fish bearing streams that are tributaries to resident and anadromous salmonid streams, site specific buffers on flood plains and alluvial streams, management of fish streams "to preserve biological integrity", and implementation of watershed analysis. The results and recommendations from the Anadromous Fish Habitat Assessment Report formed the cornerstone for the provisions for fish stream and watershed management in the Revision of the Tongass Land Management Plan (TLMP 1997).

1997

In May 1997, the revision of the Tongass Land Management Plan (TLMP) was completed and included increased protection for watersheds and associated riparian areas (TLMP 1997). A significant element of the TLMP is to consider fish habitat in the context of the whole watershed from the headwaters to the ocean during management planning. The plan directly addresses riparian areas and assigns management objectives that include maintaining natural conditions for fish and aquatic life, managing for biodiversity, and to maintain streambank and stream channel processes (TLMP 1997). In most floodplain stream reaches, buffer areas are required over the active floodplain. Changes to prescribed riparian buffers require a watershed analysis to assess "important riparian and aquatic habitat values and geomorphic processes within a watershed". While maintaining and reinforcing protection afforded to anadromous salmonid — class I streams, resident salmonid —class II streams, and non-fish —class III streams, TLMP identifies an additional group of streams—Class IV streams. These include intermittent, ephemeral, and small perennial channels with low flows or low sediment transport capabilities. Although these are not specifically addressed for riparian protection, buffer strips in V-notches of higher gradient class III streams, which may be ephemeral, are included. The management strategy of the standards and guides is to retain natural stream function and processes in watersheds that fall into management categories that will be used for timber harvest or other development activities.

History of Timber Harvest

Timber harvest in southeast Alaska was not located randomly throughout time or location (TLMP Revision 1997). The sites with easy access and high volumes of wood were harvested first. High volume timber sites were frequently located in the valley bottoms less than 244 m (800 ft) in elevation and along riparian corridors. More than 70% of the total timber volume on the TNF was harvested from 1950 through 1982, the period when minimum riparian protection was given to streams (Table 1). Of the 156,600 ha (387,000 acres) logged from 1950 through 1994, 38% (59,896 ha) were harvested from 1950 through 1970 (Table 1). Furthermore, timber harvest was concentrated on selected islands such as Chichagof, Kuiu, Prince of Wales, and Revillagigado islands (Figure 3). Other locations such as Admiralty Island, most of which has been designated as a National Monument, and Baranof Island which contains large wilderness areas, are less developed. They also contain extensive areas of non-commercial forests.

During the first 20 years of large scale timber harvest, most harvest occurred in the valley bottoms where low gradient streams are located. These

TABLE 1. Timber harvest of the Tongass National Forest by time period and by elevation.

Time period	Area in hectares and (percent harvested) during each time period			
		Elevation (m)		
	Total	<244	244-457	>457
1950-70	59,896	54027.6 (90.2)	5665.8 (9.5)	202.35 (0.34)
1971-1982	53,420	45164.5 (84.5)	8094.0 (15.2)	161.88 (0.30)
1983-1990	28,329	20639.7 (73.6)	6879.9 (24.5)	526.11 (1.88)
1991-1994	14,974	9308.1 (62.2)	5261.1 (35.1)	404.7 (2.70)

streams and their associated riparian habitats (i.e. beaver ponds) also are the most productive locations for anadromous salmonids. From 1950 to 1970, 90% of the total area harvested was less than 244 m in elevation (Table 1). As timber harvest progressed, proportionally more area above 244 m was harvested and by 1991 more than 37% of the timber harvest occurred above 244 m in elevation (Table 1). Less than 30% of the area was harvested while measures were in place that recognized small rearing streams and afforded increased protection to non-anadromous species. Less than 10% of the total area was harvested when buffer strips were an integral and required part of watershed management.

Maybeso Creek, located on Prince of Wales Island, was harvested during the 1950's. Harvest began at the bottom of the valley and continued up to 366 m (1,200 ft) in elevation during one entry (Figure 4). All merchantable timber along the riparian zone was harvested which was the general pattern of harvest for the first 20 years of timber harvest. In subsequent years, harvest patterns changed and by 1970 smaller patches (usually < 40 ha) were cut. The earlier harvest units tended to be in the valley bottoms. Most of the harvest units during 1974 through 1976 in the Corner Creek watershed were located along the stream, whereas, those cut in 1986 or later were located at higher elevations away from the main channel (Figure 5). A similar pattern occurred in the Hamilton Creek watershed with later units placed further upstream and on higher elevations (Figure 6). The concentration of intense timber harvest in the riparian zone before 1980 left a legacy of watersheds with little or no riparian protection.

The effect of time and elevation of timber harvest is reflected in the number of kilometers of stream that were within 100 m of a timber harvest unit. More than 75% of the length of anadromous streams were near or adjacent to a timber harvest unit that was cut from 1950 to 1982 (Table 2). As changes in forest management that moved harvest units away from the riparian zone were implemented, the amount of harvest in these areas decreased. The largest part of timber harvest occurred in the valley bottoms adjacent to streams before adequate management practices were in place to reduce even the most obvious detrimental effects of timber harvest on stream habitats.

The Persistence of Salmon

Despite the legacy of watersheds that were logged with poor riparian management practices throughout southeast Alaska, such as the Maybeso Creek watershed, few documented declines of salmon stocks are recorded (Baker et al. 1996). However, few watersheds in southeast Alaska have escapement records that are dependable before 1960 and no systematic or quantitative studies document juvenile or smolt numbers from watersheds before the onset of large scale logging in southeast Alaska (Halupka et al. in press).

Natural fluctuations at a region-wide scale caused by changes in marine survival, weather cycles, or other environmental factors as well as production of salmon from intact watersheds will obscure declines in a single watershed. The limitations of catch statistics as indicators of stock abundance are generally acknowledged (see Bisson et al. 1992), but the cycles of the commercial catch of coho salmon from 1893 through 1998 demonstrate the magnitude of region-wide variation that obscure trends

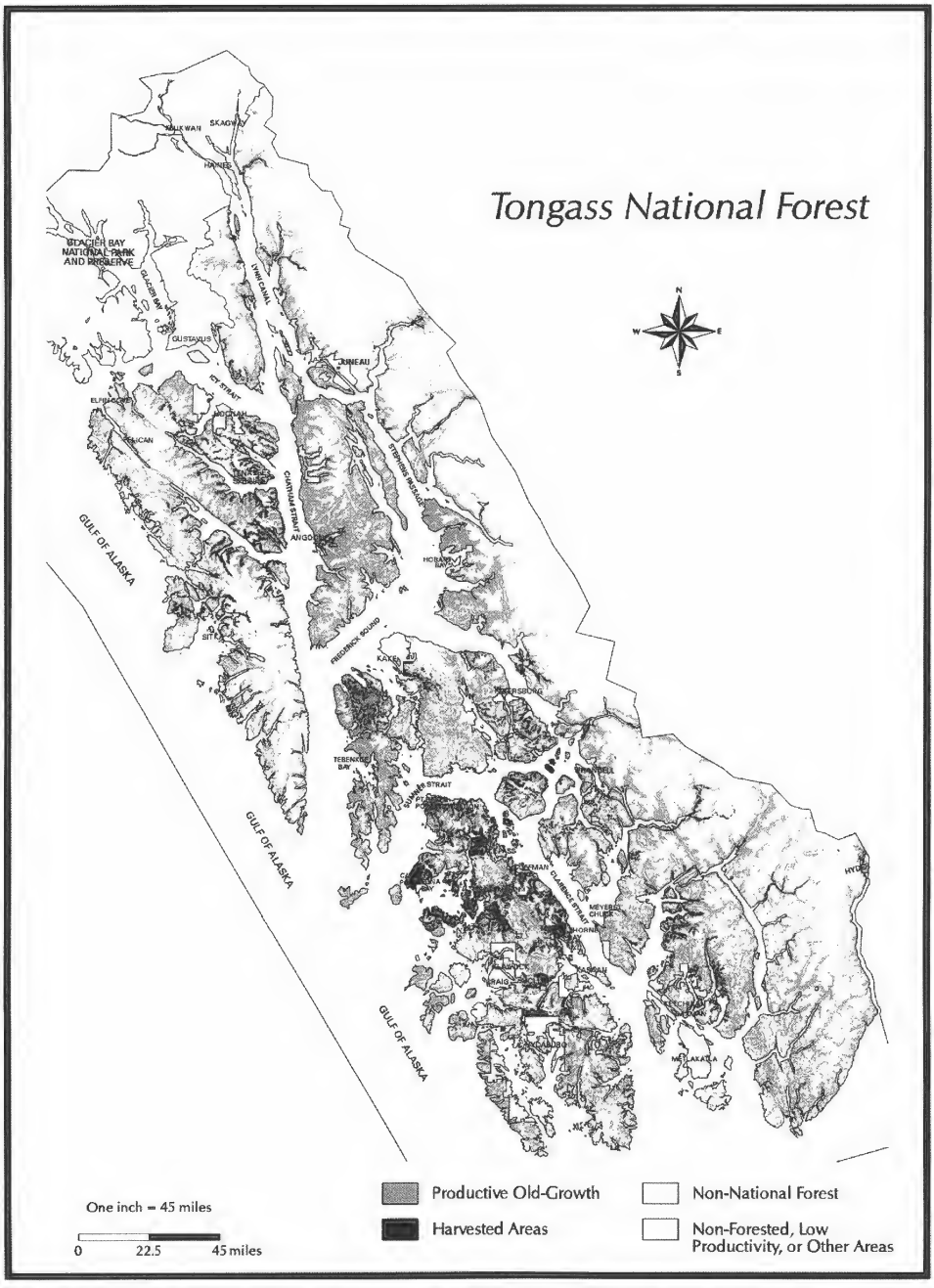


Figure 3. Distribution of commercial old-growth forest and timber harvest throughout southeast Alaska. "Productive Old-growth" was defined as forest cover of old-growth Sitka Spruce and Hemlock ≥ 22.8 cm (9 in) diameter breast height (dbh) and >150 years old at a volume of > 8 million board feet/acre. Timber harvest on non-National Forest land is not identified.

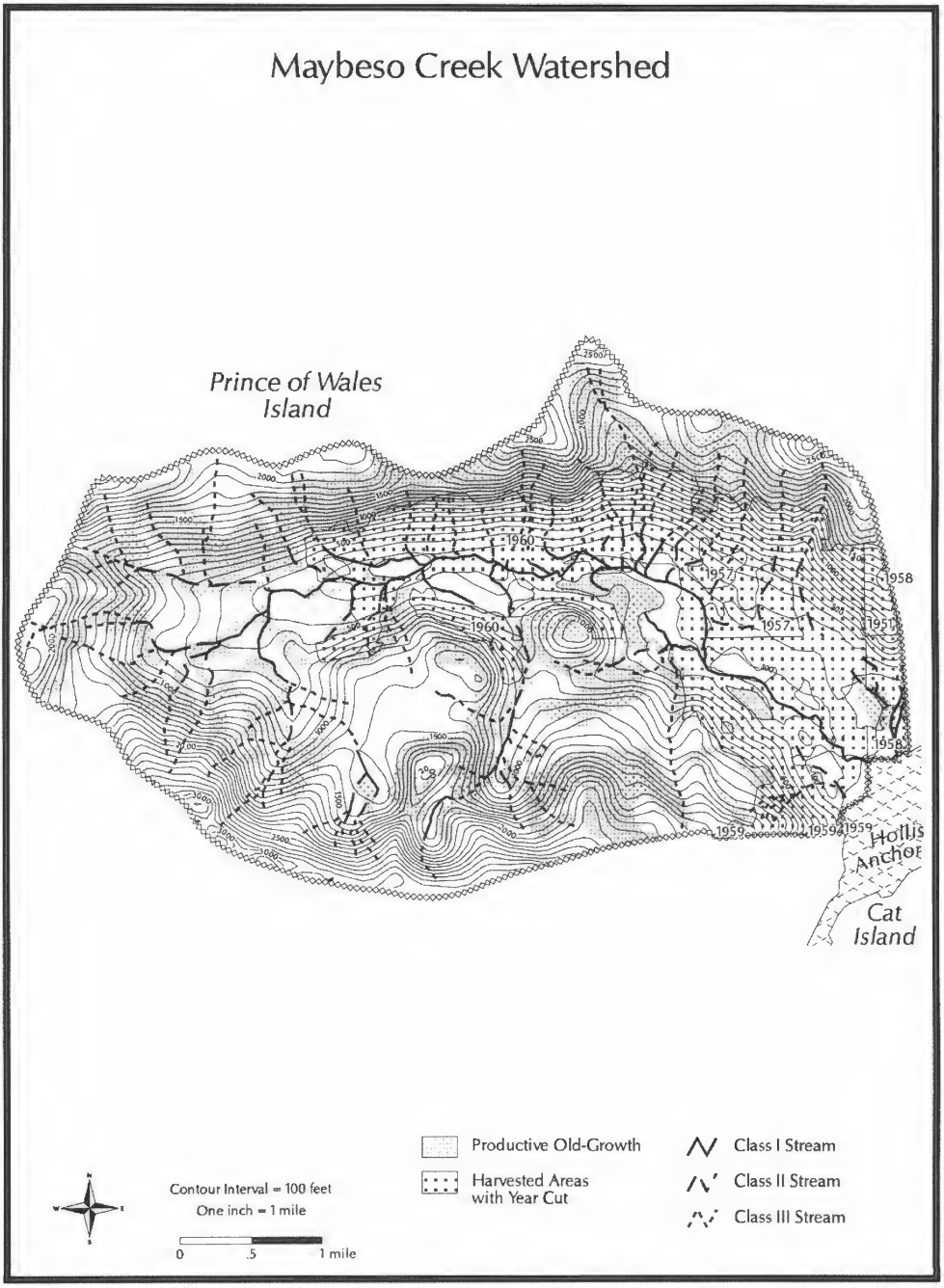


Figure 4. Timber harvest, dates of harvest, and remaining old-growth forest on the Maybeso Creek watershed, Prince of Wales Island.

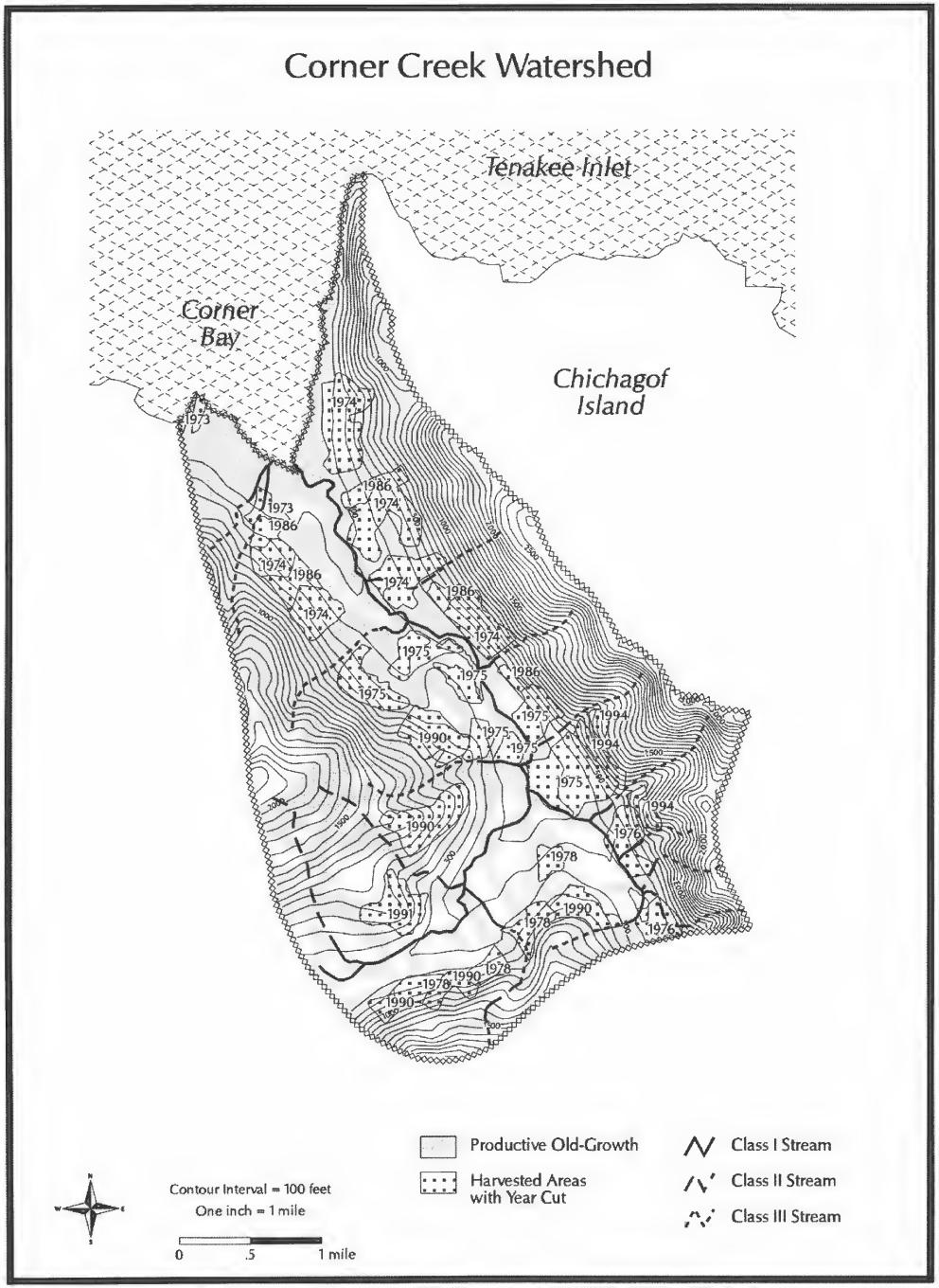


Figure 5. Timber harvest, dates of harvest, and remaining old-growth forest on the Corner Creek watershed, Chichagof Island.

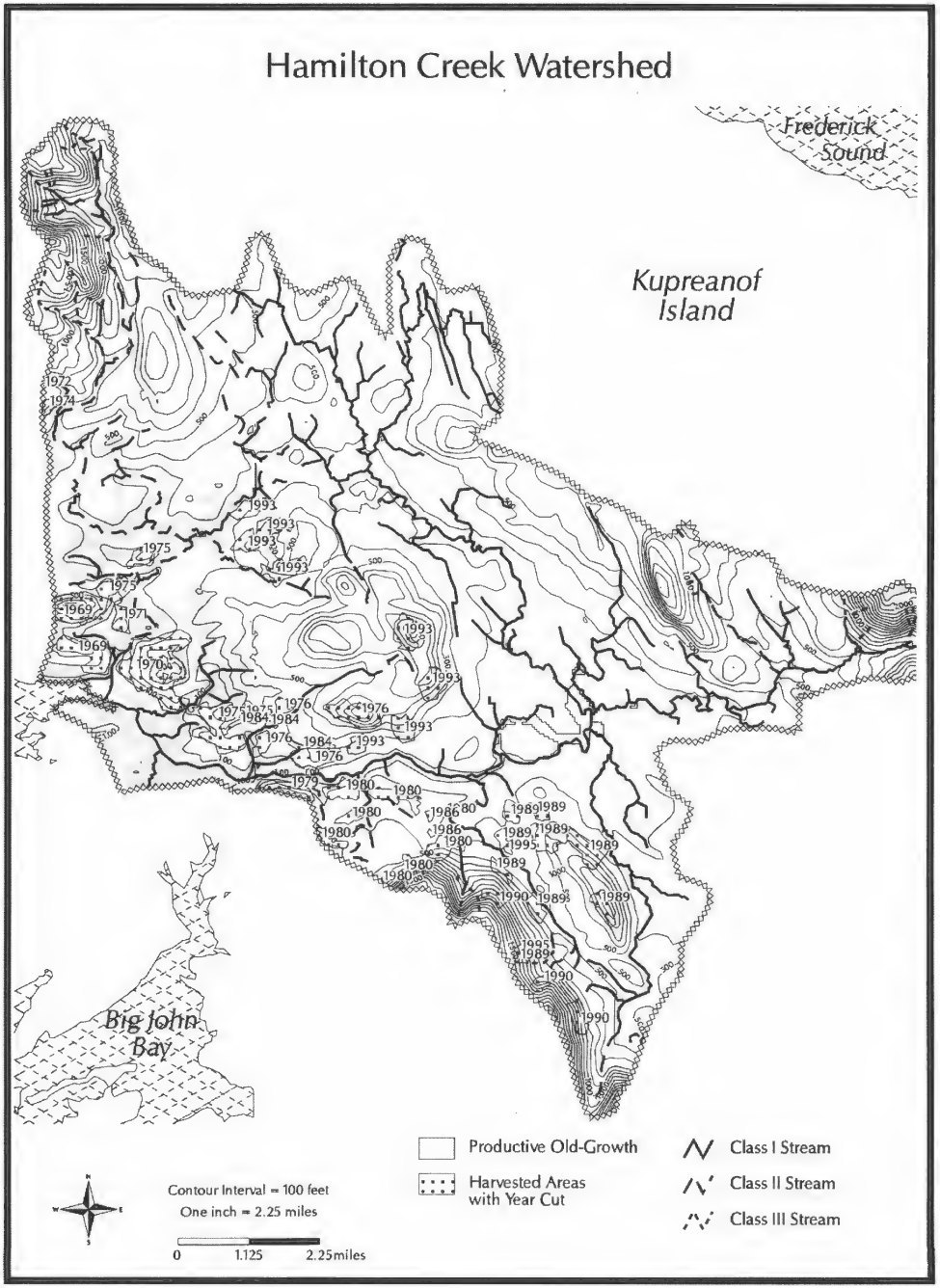


Figure 6. Timber harvest, dates of harvest, and remaining old-growth forest on the Hamilton River watershed, Kupreanof Island.

TABLE 2. Kilometers and (percent) of anadromous and non-anadromous streams within 100 m of a timber harvest unit.

Year Harvested	Anadromous (Class I) Streams	Resident Class II Streams	Total
1950-1970	880.3 (44)	326.8 (32)	1207.9 (40)
1971-1982	678.0 (34)	372.6 (38)	1051.2 (35)
1983-1990	114.4 (6)	127.0 (13)	241.5 (8)
1991-1995	319.8 (16)	189.1 (19)	509.2 (17)

for individual watersheds (Figure 7). As a result, any declines in salmon production in individual watersheds have gone undetected.

High marine survival rates during the past decade have been implicated in increased catch and escapement to all watersheds (Hofmeister et al. 1988; Shaul 1994; Beamish et al. 1997). Changes in marine survival will have a large effect on adult returns and increased marine survival will offset decreased freshwater survival as a result of habitat loss in individual watersheds. For example, estimates from Hugh Smith Lake in southeast Alaska were 51,789 smolt for 1983 and 23,499 smolt for 1985; the estimated marine survival rates for the two years were 7.4% and 19.1%, respectively (Shaul 1994). Adult returns, using these two survival estimates, were 3,832 fish in 1983 and 4,488 fish in 1985. The higher marine survival in 1985 produced a higher return from 50% fewer smolts. An increase in marine survival can easily mask a 50% loss of juvenile salmonid production in freshwater.

The effects of logging on salmon populations under various management prescriptions and particularly in watersheds with poor protection of riparian and stream habitat have been documented and reviewed in several sources (Salo and Cundy 1987; Meehan 1991; Hicks et al. 1991; Bisson et al.1992; Woodsmith and Buffington 1996). Habitat loss and reduced survival of anadromous salmonids have been documented in several studies of

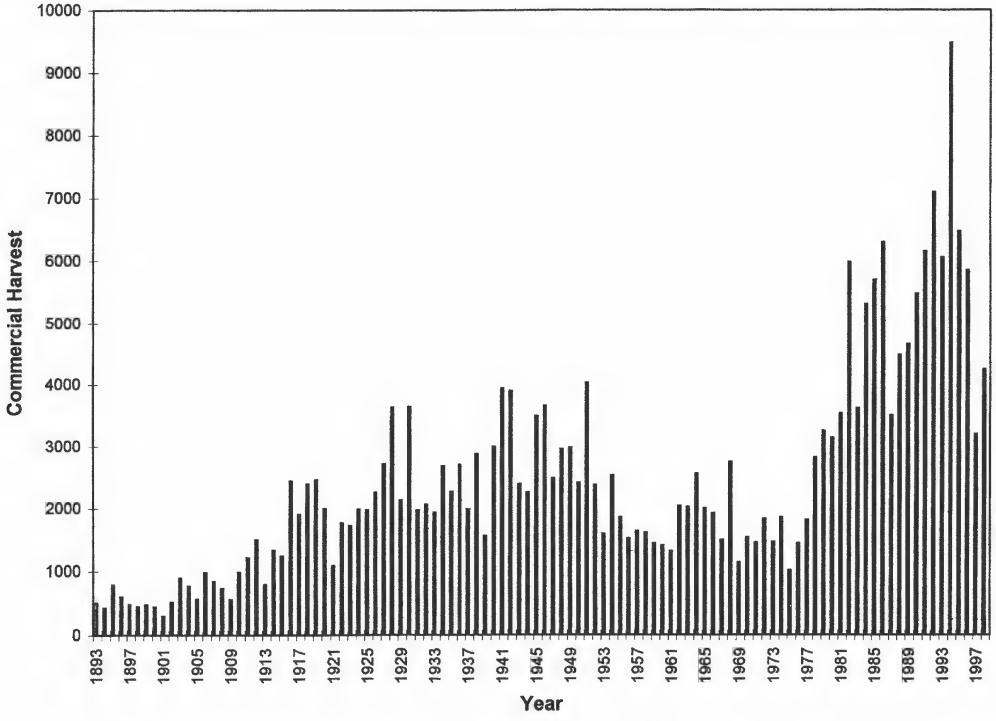


Figure 7. Annual commercial harvest of coho salmon in southeast Alaska from 1900 through 1992 (Rigby et al. 1991 and unpublished data Alaska Department of Fish and Game, Division of Commercial Fisheries, Juneau, AK).

watersheds in southeast Alaska that were logged before 1980 (Bryant 1985a; Thedinga et al. 1989; Montgomery et al.1995). The common theme among these studies is loss of stream channel complexity and simplification of habitat. However, even in intensively logged watersheds, populations of anadromous salmonids remain, but these populations are closely linked with complex habitats maintained by large wood (Dolloff 1983; Bryant 1985a). These complex habitats have been maintained by large wood that was present in streams before timber harvest. For example, in severely impacted watersheds, such as Maybeso Creek and the Harris River, large wood from old-growth trees that fell into the stream before logging provide the only anchors for large wood accumulations. The residence time of large trees in stream channels of southeast Alaska spans decades (Swanson et al. 1984; Murphy and Koski 1989) and the effects of their loss will be gradual and appear decades after the cessation of timber harvest in the watershed (Bryant 1980). A commonly accepted misconception is that stream recovery begins shortly after the cessation of activity in the watershed. In reality, the loss of habitat quality is likely to continue for more than 100 years after logging until riparian trees become large enough to maintain stream channel complexity (Bryant 1980; 1985a; Beechie et al. 1994).

Persistence of fish in some of the more severely affected watersheds can be attributed to escapements which fully seed available habitats, and the ability of some species of salmonids, coho salmon in particular, to exploit marginal habitats. The presence and expansion of beaver pond habitats in intensively logged watersheds may be an important factor maintaining coho salmon population in some of these watersheds (Bryant 1985b; Sampson 1994). Small, low gradient 2nd to 3rd order tributaries, often less than 2 meters in width, are common rearing habitat for juvenile coho salmon in southeast Alaska (Elliott and Hubbartt 1978). The size of the tributaries may allow retention of smaller wood debris (Bilby 1985). Small streams with greater amounts of large wood in intensively managed watersheds maintain higher densities of juvenile coho salmon than those with smaller amounts of wood and few pools (Dolloff 1983). The persistence of salmonids in larger watersheds is maintained by complexity that includes both instream structure, most of which is related to residual large wood, and heterogeneity of habitats within watersheds which includes a mixture of off-channel habitats, beaver ponds, and small tributaries.

On a region-wide scale, the existence and retention of intact watersheds may be a significant factor in maintaining the current status of salmon stocks in southeast Alaska. More than 75% of the Tongass National Forest is classified into Land Use Designations (LUD) I or II which include wilderness areas, National Monuments, and roadless areas (Tongass Land Management Revision 1997). This includes a substantial part of Admiralty Island and the Misty Fjord which are designated as National Monuments. Although large portions of the area in LUD I and LUD II categories are alpine, glacial, or areas of marginal economic value with respect to timber harvest, numerous highly productive watersheds in old-growth forests are also included in these designations. The watersheds in these protected landscapes represent the largest group of intact watersheds in the northern hemisphere. Other designations are LUD III which is primarily recreation use and LUD IV which allows intensive resource use such as timber harvest and mining.

The existence of these low impact land use designations (LUD I, III, and III) has resulted in a relatively high percent of anadromous streams (56%) —measured by length— that are located in watersheds that have not been affected by timber harvest (Figure 8). A total of 9,911 km (6,160 miles) (or 44%) of anadromous stream flow through watersheds that have been exposed to varying degrees of timber harvest. Of this group of watersheds, 6% of the stream length is located in watersheds that have had more than 20% of the area logged. These are likely to be the most severely affected stream systems. The largest percent of anadromous stream length is in watersheds with less than 20% of the area logged (Figure 8). While it is likely that habitat has been lost in these systems, especially in the most intensively harvested watersheds such as Maybeso Creek (Bryant 1980; 1985a), a decrease in the number of fish may be obscured by natural fluctuations and by production of fish from intact streams on a region-wide basis.

We propose the following hypothesis: 1) anadromous salmon production—measured by smolt output—will be more variable in intensively logged (>20% of area) watersheds than in intact

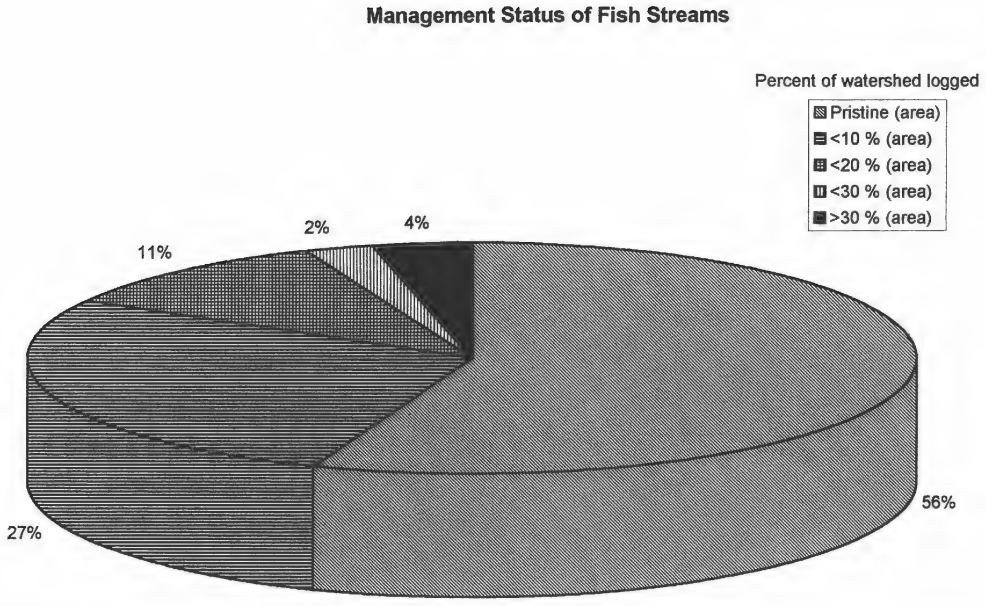


Figure 8. Relative length (%) of anadromous streams flowing through watersheds with varying percent of area logged in the Tongass National Forest.

watersheds; 2) decreases in marine survival, including natural and fishing mortality, will contribute to greater variability of smolt production in intensively managed watershed than in intact watersheds; and 3) environmental disturbances—droughts, severe floods, landslides—will have a proportionally greater effect on variability in intensively managed watersheds than in intact watersheds. The unifying theme in these hypothesis is the test of resiliency of watersheds and the prediction that intensively managed watershed will be less resilient than intact watersheds. The outcome is that salmon production in watersheds that have been intensively logged such as those during the first 30 years of industrial timber harvest in southeast Alaska may not be measurably different than many intact watersheds during benign environmental conditions and high ocean productivity, but are likely to be less resistant to adverse effects during periods of environmental stress. The streams in the unmanaged (i.e. pristine) watersheds are likely to be the most effective buffer for freshwater production of anadromous salmon region-wide.

Summary

Although "Best Management Practices" have substantially improved during the past 40 years of commercial timber harvest in southeast Alaska, most timber harvest on the Tongass National Forest occurred during the first 20 years of industrial logging and was disproportionately distributed in the valley bottoms before adequate riparian protection was in place. As a result, a legacy of watersheds with second-growth vegetation with limited potential for recruitment of large wood, as well as other adverse effects rising from poor timber harvest practices remains. While loss of salmonid production from these watersheds may be significant, it has been undocumented. However, more than 50% of the length of anadromous stream habitat remains in pristine watersheds of the Tongass National Forest. The number and distribution of intact watersheds in the TNF are critical elements for sustainable salmon populations in the face of habitat loss elsewhere in southeast Alaska and the Pacific Northwest.

The catastrophic declines in salmon stocks that have occurred in other areas of the Pacific Northwest are the result of multiple effects that include urban and agricultural development, timber harvest practices, and large dams such as those on the Columbia River which may have been exacerbated by cyclical decreases in marine productivity (Bisson et al. 1992). Furthermore, the patchwork of landowners along nearly all the watersheds of the Pacific Northwest complicates watershed management and restoration (Kohonen 1996). The multiple effects present in the Pacific Northwest are generally absent in southeast Alaska; therefore, the prospect of sustainable salmon stocks in southeast Alaska is good, but depends on a combinations of factors. The retention of existing intact watersheds is a key element. Improving riparian management in managed watersheds is important to prevent further loss of aquatic productivity. A systematic and well-planned and monitored watershed restoration effort is possible and could accelerate the recovery of damaged watersheds. A continuing conservative harvest strategy on salmon that accommodates changes in marine and freshwater conditions to allow spawning escapements that maintain freshwater productivity is essential.

Globally, few intact watersheds remain in the northern hemisphere and nearly all are in the northern regions of the hemisphere (Dynesius and Nilsson 1994; Arthington and Welcome 1995). Most of the remaining intact watersheds of the temperate rain forest occur in southeast Alaska. As the land base within southeast Alaska is further separated into old-growth forests and nonforest land, the relative amount of unmanaged old-growth forest becomes smaller. The relatively small proportion of old-growth forests supports some of the most productive salmonid habitats in North America, and a disproportionately large segment of the salmonid fishery value for the Pacific Northwest. Furthermore, these watersheds represent calibration sites for management of disturbed watersheds within the northern temperate zone and are of global significance.

Acknowledgements

We thank Francis Biles and John Day for their assistance with extracting information from the GIS database and constructing maps of southeast Alaska and of the watersheds. Rachel Baker greatly assisted with a comprehensive summary of forest management practices in the Tongass National Forest. Ron Dunlap assisted with data collection and reviewed the manuscript. Doug Swanston reviewed an earlier draft.

Literature Cited

Alaback, P. B. 1980. Biomass and production of understory vegetation in seral Sitka spruce-western hemlock forest of southeast Alaska. Ph.D. Dissertation, Oregon State University, Corvallis OR.

_____. 1991. Comparative ecology temperate rainforests of the Americas along analogous climatic gradients. Revista Chilena de Historia Natural 64:399-412.

Anderson, L. and M. D. Bryant. 1980. Fish passage at road crossings: An Annotated bibliography. General Technical Report PNW-117. U. S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.

Arthington, A. H. and R. L. Welcomme. 1995. The condition of large river systems of the world. *In* N. B. Armantrout (ed.) Condition of the worlds aquatic habitats: Proceedings of the World Fisheries Congress, Theme 1. Oxford & IBH Publishing Company, Ltd., New Delhi. Pp. 44-75.

Baker, T. T., A. C. Wertheirmer, R. D. Burkett, R. Dunlap, D. M. Eggers, E. J. Fritts, A. J. Gharret, R. A. Holmes, and R. L. Wilmot. 1996. Status of Pacific Salmon and Steelhead escapements in Southeastern Alaska. Fisheries 21(10):6-18.

Beamish, R. J., C. M. Neville, and A. J. Cass. 1997. Production of Fraser River sockeye salmon (*Oncorhynchus nerka*) in relation to decadal-scale changes in the climate and the ocean. Canadian Journal of Fisheries and Aquatic Sciences 54:543-554.

Beechie, T., E. Beamer, and L. Wasserman. 1994. Estimating coho salmon rearing habitat and smolt production losses in a large river basin, and implications for habitat restoration. North American Journal of Fisheries Management. 14:797-811.

Benda, L. 1990. The influence of debris flows on channels and valley floors in the Oregon Coast Range, USA. Earth Surface Processes and Landforms. 15:457-466.

Bilby, R. E. 1985. Influence of stream size on the function and characteristics of large organic debris. *In* Proceedings of the west coast meeting of the National Council of the Paper Industry for air and stream improvement. National Council of the Paper Industry for Air and stream Improvement, Portland, OR.

Bisson, P. A., T. P. Quinn, G. H. Reeves, and S. V. Gregory. 1992. Best management practices, cumulative effects, and long term trends in fish abundance in Pacific Northwest river systems. *In* R. J. Naiman (ed.) Watershed management: Balancing sustainability and environmental change. Springer-Verlag, New York. Pp. 189-232.

Bryant, M. D. 1980. Evolution of large, organic debris after timber harvest: Maybeso Creek, 1949 to 1978. General Technical Report PNW-101. U. S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.

_____. 1983. The role and management of woody debris in west coast salmonid nursery streams. North American Journal of Fisheries Management 3:322-330.

_____. 1985a. Changes 30 years after logging in large woody debris, and its use by salmonids. *In* R. Johnson, C. D. Ziebell, D. R. Patton, P. F. Ffolliott, and R. H. Hamre. (eds.) Riparian Ecosystems and their management: Reconciling conflicting uses. General Technical Report RM-120. U.S. Department of Agriculture, U. S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. Pp. 329-334.

_____. 1985b. The role of beaver dams as coho salmon habitat in southeast Alaska streams. *In* J. M. Walton and D. B. Houston. (eds.) Proceedings of the Olympic wild fish conference. Fisheries Technology Program Peninsula College and Olympic National Park, Port Angeles, WA. Pp. 183-192.

Cederholm, C. J., D. B. Houston, D. L. Cole, and W. J. Scarlett. 1989. Fate of coho salmon carcasses in spawning streams. Canadian Journal of Fisheries and Aquatic Sciences. 46:1347-1355.

Dane, B. G. 1978. Culvert guidelines: Recommendations for the design and installation of culverts in British Columbia to avoid conflict with anadromous fish. Technical Report No. 811. Department of Fish and Environment, Pacific Region, Fisheries and Marine Service. Vancouver, B.C.

Dolloff, C. A. 1983. The relationships of wood debris to juvenile salmonid production and microhabitat selection in small southeast Alaska streams. Ph.D. Dissertation, Montana State University, Bozeman.

Dynesius, M. and C. Nilsson. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. Science 266:753-762.

Ecotrust, Pacific GIS, and Conservation International. 1995. The rain forests of home: An atlas of people and place. Part 1: Natural forests and native languages of the coastal temperate rainforest. Portland, OR.

Elliott, S. T. and D., Hubbartt. 1978. A Study of land use activities and their relationship to sport fish resources in southeast Alaska. Alaska Department of Fish and Game, Sport Fish Division. Federal Aid in Fish Restoration D-1, Vol. 19. Juneau, AK.

Forest Ecosystem Management Team (FEMAT). 1993. Forest ecosystem management: An ecological, economic, and social assessment. U.S. Department of the Agriculture, Forest Service, U.S. Department of Interior, Fish and Wildlife Service, Bureau of Land Management, and National Park Service, U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, and Environmental Protection Agency, Washington, D.C.

Hagenstein, R. H. 1993. A report on the coastal temperate rain forest: Geographic Information system with emphasis on Alaska's Prince William Sound. Ecotrust Inc. Portland, OR 21p.

Halupka, K. C., M. D. Bryant, M. F. Willson, and F. H. Everest. In Press. Biological status and population status of anadromous salmonids in Southeast Alaska. General Technical Report. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.

Harris, A. S. and W. A. Farr. 1974. The forest ecosystem of southeast Alaska: 7. Forest ecology and timber management. USDA Forest Service General Technical Report PNW-25. U.S.D.A. Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, OR.

Harris, A. S., O. K. Hutchinson, W. Meehan, D. N. Swanston, A. E. Helmers, J. C. Hendee, and T. M. Collins. 1974. The forest ecosystem of southeast Alaska: 1. The setting. U.S.D.A. Forest Service General Technical Report PNW-12. Pacific Northwest Forest and Research Station, Portland, OR.

Heede, B. H. 1972. Influences of a forest on the hydraulic geometry of two mountain streams. Water Resources Bulletin. 8(3):523-530.

Heusser, C. J. 1960. Late-pleistocene environments of north Pacific America. American Geographic Society Special Publication No. 35.

Hicks, B. J., J. D. Hall, P. A. Bisson, and J. R. Sedell. 1991. Responses of salmonids to habitat changes. *In* W. R., Meehan (ed.) Influences of forest and rangeland management. Pp. 483-518.

Hofmeister, K., J. R. Dangle, and J. D. Jones. 1988. Southeast Alaska pink and chum investigations, 1987-88. Federal Aid Contract No. Na-87-ABD-00301. Alaska Department of Fish and Game, Division of Commercial Fisheries. Regional information report No. 1J88-38. Juneau, Alaska.

Keller, E. A. and T. Talley. 1979. Effects of large organic debris on channel form and fluvial processes in the coastal redwood environment. *In* D. D. Rhodes and G. P. Williams. (eds.) Adjustments of the fluvial system. Kendall/Hunt Publishing Company, Dubuque, Iowa. Pp. 169-197.

Korhonen, I. M. 1996. Riverine ecosystems in international law. Natural Resources Journal 36:515-553.

Lamberti, G. A., S. V. Gregory, L. R. Ashkenas, R. C. Wildman, and K. M. S. Moore. 1991. Stream recovery following a catastrophic debris flow. Canadian Journal of Fisheries and Aquatic Sciences. 48:196-208.

Lehmkuhl, J. F. and L. F. Ruggiero. 1991. Forest Fragmentation in the Pacific Northwest and its potential effects on wildlife. *In* L. F. Ruggiero, K. B. Aubrey, A. B. Carey, and M. H. Huff. (eds.) Wildlife and vegetation of unmanaged Douglas-Fir forests. General Technical Report PNW-GTR-285, U. S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. Portland, Oregon. Pp. 35-46.

McDougall, W. A. 1993. Let the sea make a noise. A history of the North Pacific from Magellan to MacArthur. Basic Books, New York.

McIntosh, B. A., J. R. Sedell, J. E. Smith, R. C. Wissmar, S. E. Clarke, G. H. Reeves, and L. A. Brown. 1994. Historical changes in fish habitat for select river basins of Eastern Oregon and Washington. Northwest Science 68:36-53.

Meehan, W. R. 1974. The forest ecosystem of southeast Alaska: 3. Fish Habitats. General Technical Report PNW-15, U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. Portland, OR.

_____. 1991. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society Special Publication 19. Bethesda, MD.

Mills, D. 1991. Ecology and Management of Atlantic Salmon. Chapman & Hall, London.

Montgomery, D. R., J. M. Buffington, R. D. Smith, K. M. Schmidt, and G. Pess. 1995. Pool spacing in forest channels. Water Resources Research 31:1097-1105.

Murphy, M. L. and K. V. Koski. 1989. Input and depletion of woody debris in Alaska streams and implications for streamside management. North American Journal of Fisheries Management 9:427-436.

Murray, T. and & Associates. 1970. Alaska's commercial timber resource. Alaska Department of Economic Development, Juneau, Alaska.

Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: Stocks at risk from California, Oregon, Idaho, and Washington. Fisheries 16(2):4-21.

Petts, G. 1989. Historical analysis of fluvial hydrosystems. *In* G. E. Petts, H. Moller, and A. L. Roux (eds.) Historical change of large alluvial rivers: Western Europe. John C. Wiley & Sons, Chichester, UK. Pp. 1-18.

Petts, G., H. Moller, and A. L. Roux. (eds.) 1989. Historical Change of large alluvial rivers: Western Europe. John Wiley & Sons, Chichester, UK.

Pewe, T. L. 1975. Quaternary geology of Alaska. Geological Survey Professional Paper 835. United States Government Printing Office. Washington, D.C.

Pielou, E. C. 1992. After the ice age. The University of Chicago Press, Chicago. 366p.

Rigby, P., J. McConnaughey, and H. Savikko. 1991. Alaska Commercial Salmon Catches, 1878-1991. Regional information report, No. 5J91-16, Alaska Department of Fish and Game, Division of Commercial Fisheries, Juneau, AK.

Ruderman, F. K. 1985. Volume and average price of selected species on the National Forests of the Pacific Northwest Region, 1973 to 1984. Research Note PNW-RN-446. U.S. Department of Agriculture, Forest Service. Pacific Northwest Research Station, Portland, OR.

Salo, E. O. and T. W. Cundy. 1987. Streamside management: Forestry and fishery interactions. Proceedings of a symposium: 12-14 February 1986. University of Washington, Seattle.

Sampson, J. R. 1994. The distribution and habitat value of wetlands created by beaver (*Astor canadensis*) in southeast Alaska. M.S. Thesis, University of Washington, Seattle, WA.

Schmiege, D. C., A. E. Helmers, and D. M. Bishop. 1974. The forest ecosystem of southeast Alaska: 8. Water. USDA Forest Service General Technical Report PNW-28. Pacific Northwest Forest and Range Experiment Station, Portland, OR.

Shaul, L. 1994. A summary of 1982-1991 harvest, escapement, migratory patterns, and marine survival rates of coho salmon stocks in southeast Alaska. Alaska Fishery Research Bulletin 1:10-32.

Shochat, E. 1993. Altering Alaska salmon habitat and natural history: potential impacts on bald eagles and other vertebrates. B.A. Thesis, Rutgers College, New Brunswick, N.J.

Slaney, T. L., K. D. Hyatt, T. G. Northcote, and R. J. Fielden. 1996. Status of anadromous salmon and trout in British Columbia and Yukon. Fisheries 21(10):20-35.

Stolte, L. 1981. The forgotten salmon of the Merrimack. U.S. Department of the Interior, Northeast Region, Washington, D.C.

Swanson, F. J., G. W. Lienkaemper, and J. R. Sedell. 1976. History, physical effects, and management implications of large organic debris in western Oregon. General Technical Report PNW-56. U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, OR.

Swanson, F. J., M. D. Bryant, G. W. Lienkaemper, and J. R. Sedell. 1984. Organic debris in small streams, Prince of Wales Island, southeast Alaska. General Technical Report PNW-166. U. S. Department of Agriculture, Forest Service, Pacific Northwest Forest Research Station, Portland, OR.

Thedinga, J. F., M. L. Murphy, J. Heifetz, K. V. Koski, and S. W. Johnson. 1989. Effects of logging on size and age composition of juvenile coho salmon (*Oncorhynchus kisutch*) and density of presmolts in southeast Alaska streams. Canadian Journal of Fisheries and Aquatic Sciences 46:1383-1391.

Tongass Land Management Plan (TLMP). 1979. Final Environmental Impact Statement. U.S. Department of Agriculture, Forest Service, Alaska Region. Juneau. 312p.

_____. 1997. Land and Resource Management Plan: Tongass National Forest. Alaska Region R10-MB-338dd. U.S. Department of Agriculture, Forest Service, Region 10. Juneau, AK.

Tongass Land Management Plan Revision. 1997. Final Environmental Impact Statement. Forest Service R10-MB-338e. U.S. Department of Agriculture, Forest Service, Region 10. Juneau, AK.

Tongass Timber Reform Act. 1990. Public Law 101-626.

U.S. Department of Agriculture, Forest Service. 1960. Guide for Forest development road location, survey, design, and construction. Alaska Region 10. Juneau. 34p.

_____. 1976. Logging and fish habitat. U.S.D.A. Forest Service, Alaska Department of Fish and Game, Alaska Department of Natural Resources., Juneau, Alaska.

_____. 1983. Alaska Regional Guide and Final Environmental Impact Statement, Alaska Region Report, Region 10 Number 126 a&b. Juneau NP.

_____. 1984. Tongass Land Management Plan Evaluation Report Administrative Document 139. Alaska Region, Juneau. 165p.

_____. 1986. Forest Service Handbook 2609.24-Aquatic Habitat Management Handbook. U.S. Department of Agriculture, Forest Service, Region 10, Juneau, AK.

_____. 1993. Forest Service Handbook 2509.22: Soil and Water Conservation Handbook. U.S. Department of Agriculture, Forest Service, Alaska Region, Juneau, AK.

_____. 1995. Anadromous Fish Habitat Assessment Report. R10-MB-279. U.S. Department of Agriculture, Forest Service, Alaska Region & Pacific Northwest Research Station., Juneau.

Viereck, L. A. and E. L. Little. 1972. Alaska trees and shrubs. Agriculture Handbook No. 410. U.S. Department of Agriculture, Forest Service, Washington, D. C.

Warren, D. D. 1996. Production, price, employment, and trade in Northwest forest industries, second quarter 1996. Resource Bulletin PNW-RB-219. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.

Willson, M. F. and K. C. Halupka. 1995. Anadromous fish as keystone species in vertebrate communities. Conservation Biology 9:249-278.

Received 26 January 1998
Accepted for publication 5 November 1998

Wipfli, M .W., J. Hudson, and J. Caouette. In Press. Do salmon carcasses increase stream productivity? Canadian Journal of Fisheries and Aquatic Sciences.

Wissmar, R. C., J. E. Smith, B. A. McIntosh, H. W. Li, G. H. Reeves, and J. R. Sedell. 1994. A History of resource use and disturbance in riverine basins of eastern Oregon and Washington (Early 1800s-1990s). Northwest Science 68:1-35.

Woodsmith, R. D. and J. M., Buffington. 1996. Multivariate geomorphic analysis of Forest streams: implications for channel assessment of land use impacts on channel condition. Earth Surface Processes and Landforms 21:377-393.

Zauderer, J. 1985. The florescence of arid lands in Mesopotamia, Elam, and Central Asia: An historical perspective. *In* R., Johnson, C. D. Ziebell, D. R. Patton, P. F. Ffolliott, and R. H. Hamre. (eds.) Riparian Ecosystems and their management: Reconciling conflicting uses. General Technical Report GTR-RM-120. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. Pp. 463-466.

Joel G. Ussery, School of Resource and Environmental Management, Simon Fraser University, Burnaby, British Columbia, Canada, V5A 1S6

and

Pam G. Krannitz[1], Environment Canada, Pacific Wildlife Research Centre, 5421 Robertson Rd., RR 1 Delta, British Columbia, Canada, V4K 3N2, pamk@interchange.ubc.ca

Control of Scot's Broom (*Cytisus scoparius* (L.) Link.): The Relative Conservation Merits of Pulling versus Cutting

Abstract

The control of invasive exotic plant species in sites of high conservation value should minimize both the impacts on the ecosystem of concern and the potential for regeneration of the exotic species. We examined how the method and timing of the removal of the invasive shrub Scot's broom (*Cytisus scoparius*) affected the level of site disturbance and subsequent broom regeneration from seed and resprouting in remnant Garry oak (*Quercus garryana*) meadow communities in Victoria, British Columbia. We compared manual uprooting versus cutting at two time periods: May, when the shrub was in flower, and in July, just prior to seed dispersal. Soil disturbance, trampling, and seedling regeneration were significantly higher in plots where broom plants were uprooted as compared to plots where broom plants were cut at the base. Amount of trampling was higher in July than in May, but in July the trampled plants were exotic grasses, while in May these included fruiting stalks of native common camas (*Camassia quamash*). Resprouting of cut stems was observed in only 7 of the 75 broom stems cut and these died-back within one year. These results suggest that the preferred Scot's broom removal strategy in Garry oak meadow communities of high conservation value is to cut broom after native herbaceous species have set and distributed seed. This approach will minimize damage to native vegetation and reduce the amount of broom seedling regeneration.

Introduction

Remnant Garry oak (*Quercus garryana*) meadow communities in British Columbia are designated "critically imperiled" by the British Columbia Conservation Data Centre (Erickson 1993, and see http://www.elp.gov.bc.ca:80/wld/cdc/). Most of what is now the City of Victoria (approximately 23 km^2) was Garry oak parkland at the time of European settlement in 1842 (Roemer 1972, McMinn et al. 1976). This oak parkland was described by early settlers in the Victoria region as open prairie dominated by a rich growth of grasses and attractive and conspicuous flowering forbs under scattered individual and groves of oaks (Douglas 1842). Most of these original oak parkland ecosystems present at the time of European settlement have been destroyed by clearing for agriculture, grazing, and urban development. Hebda (1993) estimates that only 1-5% of the original extent of this community type now remains. The few remaining Garry oak parkland ecosystems are fragments in developed landscapes and have been extensively invaded by the exotic shrub Scot's broom (*Cytisus scoparius*) (Erickson 1996).

Scot's broom is an invasive *Rhizobium*-nodulated leguminous shrub, native to the British Isles and Europe, but introduced to many other countries where it has become established in a wide range of habitats (Williams 1981, Wheeler et al. 1987, Hoshovsky 1991). Scot's broom readily establishes in pastures, cultivated fields, dry scrubland, native grasslands, open forests, roadsides, and dry waterways (Gilkey 1957, Williams 1981, Johnson 1982) and has extensively invaded susceptible areas in the Pacific Northwest (Gilkey 1957, Thilenius 1968, Franklin and Dyrness 1973, Taylor 1974, Zielke et al. 1992). The spread of broom is facilitated by disturbances, such as logging, land clearing, road building, and burning (Williams 1981, Zielke et al. 1992). Scot's broom typically forms dense stands in areas where shrubs had previously been absent or were minor components of the community. They displace native herbaceous plant species and prevent the regeneration of native trees (Williams 1981, Waterhouse 1986 and 1988).

A variety of manual, mechanical, thermal, chemical, and biological techniques have been

[1]Corresponding author

© 1998 by the Northwest Scientific Association. All rights reserved.

employed to control or eradicate Scot's broom (Hoshovsky 1991 and Zielke et al. 1992 provide reviews). Manual broom removal, either by uprooting or cutting, is often used in sites of high conservation value, presumably since these methods are perceived to be the least damaging to the ecological values of the site. Manual Scot's broom removal efforts in British Columbia have not been well documented, but uprooting seems to be the preferred option. However, evidence suggests that there is an association between soil disturbance and broom regeneration from seed (Waloff 1968, Bossard 1991, Hoshovsky 1991, Smith and Harlen 1991, Zielke et al. 1992). Soil disturbance can also lead to the colonization of the site by other weedy plant species. In addition, uprooting broom can also have negative impacts on the native herbaceous vegetation on the site by exposing bulbs, corms, rhizomes, and roots to desiccation.

Although Scot's broom will resprout readily from a cut stump, sprouting potential seems to vary with the age of the plant (Miller 1992, Hebda 1994) and the season of cutting (Bossard and Rejmanek 1994). In general, sprouting is thought to be minimized by cutting broom plants during a period of maximum stress (i.e., after flowering, during seed production, and summer drought). However, Bravo (1985) advocated cutting broom before seed set to eliminate the further accumulation of seeds in the seedbank.

The goal of this study was to test whether uprooting or cutting Scot's broom was the better option for maximizing conservation of Garry oak meadow communities. Our objectives were to test the effect of the two control methods on several variables that measure impact on the plant community: 1) trampling of vegetation, 2) soil disturbance, and 3) Scot's broom seedling regeneration. We also documented whether or not cut stems of Scot's broom resprouted.

Study Area

The study occurred in a municipal park in the city of Victoria, on the southeast corner of Vancouver Island, British Columbia (48° 25' N, 123° 22' W). This 30.3 ha park contains some of the few remaining Garry oak meadow communities in the urbanized core of Greater Victoria. The climate of this region is characterized by warm, dry summers and mild, wet winters. Total precipitation is on average 650 mm annually, with approximately 95% of precipitation falling as rain (Environment Canada 1983). Mean temperatures range from a high of 15.5° C in July to a low of 4.1° C in January. Warm temperatures and low precipitation during July and August lead to a pronounced drought or moisture deficit (Chilton 1973). The annual moisture deficit in the study area is approximately 375 mm (McMinn et al. 1976).

Although anecdotal reports suggest that much of the park was open meadow beneath scattered Garry oaks until the early twentieth century, dense thickets of the native shrub snowberry (*Symphoricarpus albus*) now form the understory beneath most of the oaks. A few meadow areas containing native herbaceous plant species remain in the park, but these sites are dominated by exotic perennial grasses and are being invaded by Scot's broom (Ussery 1997). For example, the exotic perennial grasses *Agrostis capillaris* and *Dactylis glomerata* dominate most of the study area (Ussery 1997). The May treatment plots of Block 1 were dominated instead by varying proportions of the native grass *Danthonia californica*, and the exotic grasses *Cynosurus echinatus,* and *A. capillaris*.

Methods

We used a randomized block experimental design. Four meadow sites were divided into two blocks of three 6 x 3 m plots running parallel to the direction of Scot's broom invasion. Each block was randomly assigned to either May or July removal. The treatments (cut, pull, control) were then randomly assigned to the plots in each block. In the center of each 6 x 3 m plot we established a 1 x 2 m plot for data collection which allowed for a 1 m buffer against edge effects.

Scot's broom was removed on May 29, 1993, when it was in flower, and on July 15, 1993, before seed dispersal, to time removal with maximum investment of photosynthate in the above-ground shoot. Volunteers from the community were organized for the labor to mimic other Scot's broom control efforts. In 'cut' plots, volunteers were instructed to remove the above-ground portion of all Scot's broom plants greater than approximately 0.5 cm in diameter by cutting the stem as close to the ground as possible. All smaller broom plants were to be pulled. In 'pull' plots the volunteers

were asked to uproot and remove all Scot's broom plants.

No attempt was made to restrict the movement of the volunteer laborers in the plots where broom was being removed. All of the broom plants removed from each site were carried in slings by the volunteers to central collection points where the material was fed through a chipper by the staff of the Oak Bay Parks and Recreation Department. The chipped material was removed to the Oak Bay municipal compost facility.

All of the plots were revisited within a week of removal to record the area of trampling of herbaceous vegetation and soil disturbance (i.e., exposed mineral soil). We imbedded rectangles of variable dimensions to measure the area. The edges of exposed soil were distinct enough to be accurate to the nearest square centimeter. Trampled vegetation had blurry edges so that size of area trampled was estimated as accurately as possible using this method. All 1 x 2 m plots were revisited in June 1994 to count the number of newly germinated Scot's broom seedlings and record the diameter, height, and resprouting status of all cut Scot's broom stems.

Analysis of Variance (ANOVA) was used to assess the effects of treatment, season, and an interaction between treatment and season on the amount of disturbed soil and trampled vegetation, and number of Scot's broom seedlings. The error term used to test the significance of removal method and timing was the variation attributable to the interaction between the different blocks and the appropriate treatment. Because of heteroscedasticity, the ANOVA on seedling regeneration in Scot's broom was performed on rank values rather than the raw data (SAS 1990). Contingency analysis (G-test) was used to test the association of different classes of stem diameter with resprouting.

Results

The percent cover of Scot's broom ranged from 20% to 60%, with a mean of 37.5% (± 10.8%, SE). The mean density of broom stems (excluding seedlings <10 cm in height) was 15.6 (± 9.6) per $2m^2$. Height of broom plants ranged from 40 cm to 162 cm.

Trampling affected more plot area than soil disturbance (Figures 1, 2). The proportion of herbaceous vegetation in each plot that was trampled during broom removal ranged from 25% to 100%. Treatments where broom shrubs were pulled rather than cut experienced more trampling (Figure 1, F=83.55, P=0.003, df=1,3). More trampling occurred in July, once the exotic perennial grasses had matured, than in May (F=97.04, P=0.002, df=1,3). However, the plants trampled in May were of greater conservation concern as they included fruiting heads of common camas (*Camassia quamash*).

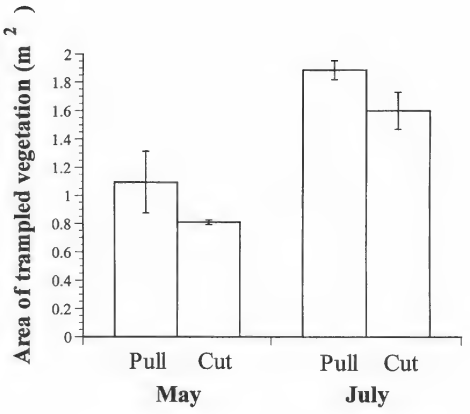


Figure 1. Area trampled per plot of Scot's broom removal, either by pulling or cutting in May or July. Means are shown ± 1 SE. Sample size is 4 plots per treatment.

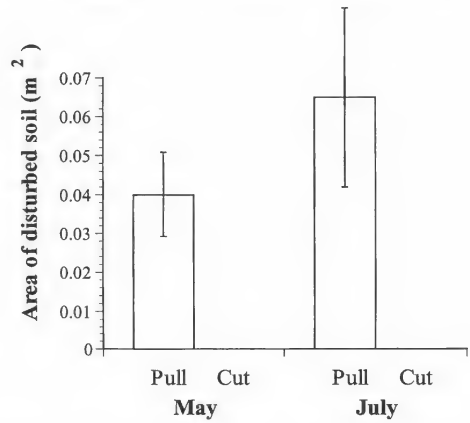


Figure 2. Area of disturbed soil per plot of Scot's broom removal in May and July. No soil was disturbed during the cutting treatments. Means are shown ± 1 SE. Sample size is 4 plots per treatment.

There was a significant relationship between the method of Scot's broom removal and the amount of soil disturbed (F=16.33, P=0.03, df=1,3). Soil disturbance was measurable in all "pull" plots, but not in "cut" plots (Figure 2). The total area of soil disturbed in "pull" plots ranged from 0.02 m^2 (1% of the plot) to 0.13 m^2 (6.5%). The timing of broom removal did not significantly affect the amount of soil disturbed (F=0.97, P=0.40, df=1,3).

More broom seedlings emerged the following spring in plots with adults removed by pulling rather than by cutting (Table 1, Figure 3). In every case, there were fewer broom seedlings in "cut" plots than in "pull" plots. Seedlings also emerged in plots that still had a canopy of adult broom plants ("control"), though fewer than in the treated plots (Figure 3). There was much variation (1-330/m^2) in the number of Scot's broom seedlings recorded within and between blocks (Table 1). The type and amount of grass cover may have affected the number of seedlings; further study will be needed to substantiate this (Ussery 1997).

Resprouting was observed in seven broom stems cut in May out of a total of 75 cut stems that were followed through the season (Table 2). Broom plants with small basal diameter were more likely to resprout upon cutting than plants with large basal diameter (Table 2). The highest rate of resprouting was 12.7 % for stems of less than 1.5 cm in diameter. The new shoots from all seven that resprouted died within the following year, so that no vegetative regeneration occurred from cut stems.

TABLE 1. ANOVA for seedling regeneration of Scot's broom following two different removal treatments (uprooting versus cutting) at two different times (late May and mid July). The r^2 of the model was 92.6%. The ANOVA was performed on rank values because of lack of homogeneity of variance.

Source	df	MS	F	P
A Block	3	171.75	A/G = 12.25	0.0057
B Treatment	2	147.22	B/D = 11.65	0.0086
C Timing	1	24.00	C/E = 0.57	0.51
D Block X Treatment	6	12.64	D/G = 0.90	0.55
E Block X Timing	3	42.19	E/G = 3.01	0.12
F Treatment X Timing	2	11.66	F/G = 0.83	0.48
G Error	6	14.02		

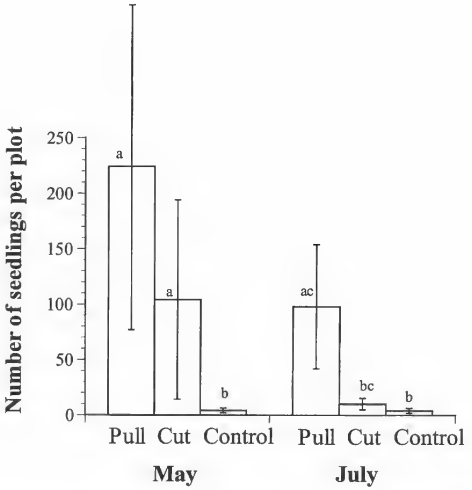


Figure 3. Number of emergent Scot's broom seedlings per plot in the year after adults were removed either in May or July, and either by pulling or cutting. Means are shown ± 1 SE. Sample size is 4 plots per treatment. Bars with different letters are significantly different at $P < 0.05$ (Fisher's Least Significant Difference Test, SAS 1990). Significant differences were calculated using rank values.

TABLE 2. Frequency of Scot's broom stem resprouting in relation to stem diameter. Expected values are in parentheses, below observed values. G-test: 12.46, df = 4, $0.025 < P < 0.01$.

Resprouting Status	Stem Diameter (mm) 1-5	6-10	11-15	16-20	21-25
Resprouted	0	5	2	0	0
	(1.4)	(1.99)	(1.4)	(0.84)	(0.37)
Not Resprouted	10	30	15	9	4
	(13.6)	(29.01)	(13.6)	(8.16)	(3.63)

Discussion

Our results suggest that cutting is a better approach than uprooting for Scot's broom control on Garry oak sites of high conservation value. Trampling, soil disturbance, and subsequent seedling regeneration were less in cut versus uprooted plots. Our results also suggest that uprooting broom to prevent vegetative regeneration through resprouting is unnecessary because resprouting can be prevented or minimized by cutting at times of the year when the plant is most stressed.

The larger area trampled in plots where Scot's broom was pulled rather than cut, could be due to the greater effort needed to uproot most broom plants. When broom plants did not pull out easily, workers would circle to pull from different directions, thereby increasing the amount of trampling. Trampling can negatively affect the growth, reproduction, and the persistence of desirable herbaceous vegetation (Chappel et al. 1971, Burden and Randerson 1972, Liddle 1975). High levels of trampling before native forbs and grasses have been able to set and disperse seed may threaten the long-term viability of native plant populations already in decline. In our study sites, late May was still too early to avoid harming native flowering bulbs, with native common camas still forming fruits and seeds. In areas with established Scot's broom plants and declining native herbs, we recommend that broom plants be cut no earlier than mid June to allow seed dispersal of species of interest.

There was little variation in the area of soil disturbed within both May and July 'pull' plots despite considerable within- and between-site differences in Scot's broom size and density, and differences also in the composition of herbaceous vegetation. These differences may have had an impact on the variation between study plots in broom seedling regeneration, but this factor will have to be substantiated with further study.

Though we can not make a direct connection between soil disturbance and seedling regeneration we can say that the act of uprooting Scot's broom plants resulted in more seedlings than did cutting. Regardless of the method of removal, a flush of Scot's broom seedlings can be expected to appear after the canopy of broom is removed (Hoshovsky 1991, Hebda 1994, Smith 1994). Scot's broom seedlings may continue to appear for years after the initial control effort and annual follow-up treatments will be required to prevent the re-establishment of the species. For example, at a site in Australia, Scot's broom seedlings were still appearing after 16 years of sustained broom removal (Smith and Harlen 1991).

The low stem resprouting rate of Scot's broom plants with stems less than 2.5 cm in diameter was an unexpected result in this study. Both Miller (1992) and Hebda (1994) have recommended pulling broom plants with stem diameters less than 2.5 cm, based on their observations that plants below this size readily resprout from the cut stem. However, seasonal differences in resprouting ability observed by Bossard and Rejmanek (1994) show minimal resprouting (0%-10%) when cut in August. These and our results suggest that Scot's broom plants of all diameters, including those less than 2.5 cm, exhibit minimal resprouting if cut during mid-summer. Bossard and Rejmanek (1994) found the highest resprouting rate (90%-100%) occurred from plants cut in January and March, a period of dormancy and abundant root reserves.

The only drawback to cutting Scot's broom stems in mid summer is that by then its seeds have matured, and removal inevitably results in dispersal of Scot's broom seeds. Scot's broom seeds are viable in the seed bank for many years (Zielke et al. 1992). In sites where broom is not yet well established there is, therefore, a concern that broom removal in the summer might inadvertently lead to spread of the local Scot's broom population. Where Scot's broom is already well established, this is less of a concern; rather the priority becomes minimizing trampling damage to the remnant native herbaceous flora.

Acknowledgements

We are grateful to the Oak Bay Parks and Recreation Department for access to Uplands Park. We thank Adolph Cêskâ, for initiating Scot's broom removal from Uplands Park, and volunteers for assistance in the field. Statistical advice was provided by Francois Bellevance and Peter Ott. Comments from Ken Lertzman, Thomas Kaye, Barry Smith and an anonymous reviewer improved an earlier version of the manuscript. Environment Canada provided funding.

Literature Cited

Bossard, C.C. 1991. The role of habitat disturbance, seed predation and ant dispersal on establishment of the exotic shrub *Cytisus scoparius* in California. Amer. Midl. Nat. 126:1-13.

Bossard, C.C. and M. Rejmanek. 1994. Herbivory, growth, seed production, and resprouting of an exotic invasive shrub *Cytisus scoparius*. Biol. Cons. 67:193-200.

Bravo, L.M. 1985. We are losing the war against broom. Fremontia 12:27-29.

Burden, R.F. and P.F. Randerson. 1972. Quantitative studies of the effects of human trampling on vegetation as an aid to the management of semi-natural areas. J. Appl. Ecol. 9:439-58.

Chappel, H.G., J.F. Ainsworth, R.A.D. Cameron, and M. Redfern. 1971. The effect of trampling on a chalk grassland ecosystem. J. Appl. Ecol. 8:869-882.

Chilton, R.R. 1973. Climatic summary for greater Victoria region. *In* C.V. Stanley Jones and W.A. Benson (eds.), An inventory of land resources and resource potentials in the Capital Regional District. A cooperative report of the British Columbia Land Inventory, Canadian Forestry Service, and Canada Department of Agriculture, Victoria, B.C. Pp. 5-22

Douglas, J. 1842. Report to McLoughlin, July 12, 1842. *In* The Beaver, Outfit 273, March, 1943. Pp. 4-9

Environment Canada. 1983. Principle station data: Victoria Gonzales Heights A. Canadian Climate Program, PSD/DSP-21. Atmospheric Environment Service, Vancouver.

Erickson, W.R. 1993. Garry oak (*Quercus garryana*). Ecosystems at Risk series. BC Ministry of Environment, Lands and Parks, Victoria, BC.

_____. 1996. Classification and interpretation of Garry oak (*Quercus garryana*) plant communities and ecosystems in southwestern British Columbia. University of Victoria, Victoria. M.S. Thesis.

Franklin, J.F. and C.T. Dyrness. 1973. Natural vegetation of Oregon and Washington. U.S. Department of Agriculture Forest Service. General Technical Report PNW-8. Portland, OR.

Gilkey, H.M. 1957. Weeds of the Pacific Northwest. Oregon State College, Corvallis, OR.

Hebda, R.J. 1993. Natural history of Garry oak (*Quercus garryana*). *In* R.G. Hebda and F. Aitkens (eds.). Proceedings of the Garry Oak Meadow Colloquium, Victoria, B.C. Garry Oak Meadow Preservation Society, Victoria, B.C.. Pp. 3-7.

___. 1994. Beating broom. Island Grower April issue, Pp. 35-37.

Hoshovsky, M. 1991. Elemental stewardship abstract for *Cytisus scoparius.* The Nature Conservancy. Arlington, Virginia.

Received 6 May 1998
Accepted for publication 27 October 1998

Johnson, P.N. 1982. Naturalized plants in southwest South Island, New Zealand. New Zeal. J. Bot. 20:131-142.

Liddle, M.J. 1975. A selective review of the ecological effects of human trampling on natural ecosystems. Biol. Cons. 7:17-36.

McMinn, R.G., S. Eis, H.E. Hirvonen, E.T. Oswald, and J.P. Senyk. 1976. Native vegetation in British Columbia's capital region. Department of Environment, Pacific Forest Research Centre, Report B.C.-X-140, Victoria, B.C.

Miller, G. 1992. Manual control of broom. Oregon Department of Agriculture. Weed Control Program. Broom/Gorse Quarterly 1(2):3-4.

Roemer, H.L. 1972. Forest vegetation and environments of the Saanich Peninsula, Vancouver Island. University of Victoria, Victoria. Ph.D. Dissertation.

SAS Institute Inc. 1990. SAS users guide, vol. 2, 4th ed. Pp. 891 - 1686. Cary, N.C.

Smith, J.M.B. 1994. The changing ecological impact of broom (*Cytisus scoparius*) at Barrington Tops, New South Wales. Plant Prot. Quar. 9:6-11.

Smith, J.M.B. and R.L. Harlen. 1991. Preliminary observations on the seed dynamics of broom (*Cytisus scoparius*) at Barrington Tops, New South Wales. Plant Prot. Quar. 6:73-98.

Taylor, T.M.C. 1974. The pea family of British Columbia. B.C. Provincial Museum Handbook No. 32. Victoria, B.C.

Thilenius, J. F. 1968. The *Quercus garryana* forest of the Willamette Valley, Oregon. Ecology 49:1124-1133.

Ussery, J.G. 1997. Managing invasive plant species in Garry oak meadow vegetation communities: a case study of Scotch broom. Simon Fraser University, Vancouver, B.C. Research Project.

Waloff, N. 1968. Studies on the insect fauna on Scotch broom, Sarcothamnus scoparius.. Adv. Ecol. Res. 5:88-208.

Waterhouse, B.M. 1986. *Cytisus scoparius* (broom) on Barrington Tops. Honours Thesis, Department of Geography and Planning, University of New England, Armidale, Australia.

____. 1988. Broom (*Cytisus scoparius*) at Barrington tops, New South Wales. Austr. Geog. Stud. 26:239-248.

Wheeler, C.T., O.T. Helgerson, D.A. Perry, and J.C. Gordon. 1987. Nitrogen fixation and biomass accumulation in plant communities dominated by *Cytisus scoparius* L. in Oregon and Scotland. J. Appl. Ecol. 24:231-237.

Williams, P.A. 1981. Aspects of the ecology of broom (*Cytisus scoparius*) in Canterbury, New Zealand. New Zeal. J. Bot. 19:31-43.

Zielke, K., J.O. Boateng, N. Caldicott, and H. Williams. 1992. Broom and gorse in British Columbia: a forestry perspective problem analysis. Silviculture Branch, Ministry of Forests. Victoria, B.C.

Reese Halter,[1] School of Forestry, The University of Melbourne, Creswick, Victoria, Australia 3363

Root Growth of *Eucalyptus pauciflora* Sieber ex Sprengel ssp. *pauciflora* on Mount Stirling, Southeastern Australia

Abstract

This present study was undertaken in order to further understand the role of root physiology of subalpine *Eucalyptus pauciflora* Sieber ex Sprengel ssp. *pauciflora* in relation to belowground temperature in Victoria, Australia. Root growth of *E. pauciflora* was examined for 31 months (December 1992-June 1995) in a mature stand at an elevation of 1545 m with a southerly aspect on Mt Stirling. Shoot growth was monitored from April 1994 to June 1995. It was found that root growth commenced in the spring at soil temperatures ≤ 1.5°C, under 550 mm of snow, at least one month before the onset of shoot growth and continued at least one month longer than shoot growth during the autumn. A one-month period of root dormancy occurred in August. The seasonal variation in root numbers of *E. pauciflora* appeared to be related mainly to soil temperature and to a lesser extent to soil water content. Moreover, there appeared to be some periodicity in root growth which was independent of the external environment on Mt Stirling.

Introduction

Soil temperature is of paramount importance in determining when tree roots are able to grow (Romberger 1963). Root growth of many coniferous and deciduous seedlings and trees usually commences and ceases at soil temperatures between 2 and 4°C (Harris 1926, Ross 1932, Wardle 1968, Hilton 1978). However, root elongation has been recorded at 0°C soil temperatures for seedlings of *Carya illinoensis* (Wangenh.) K. Koch grown in a controlled environment (Woodroof and Woodroof 1934). Also, winter root growth has been documented in *Acer saccharum* (Marsh.) (Morrow 1949) and at a soil temperature of 0.5°C under 2000 mm of snow in *Abies amabilis* (Dougl.) Forbes (Keyes 1982). A soil temperature of 35°C is evidently the upper limit for root growth in most temperate tree species (Lyr and Hoffmann 1967, Bowen 1991).

Theophrastus of Lesbos (372-284 BC) was evidently the first to report that root growth began before the onset of shoot growth (Dengler 1927). Duhamel du Monceau (1758) was first to note that root growth continued after autumn leaffall. Numerous studies have corroborated these early observations (e.g. Goff 1898, Woodroof and Woodroof 1934, Bhar et al. 1970, Kuhns et al. 1985). A variety of tree species have been shown to have two main periods of root growth; one during the spring and the other during the autumn (e.g. Resa 1878, Kinman 1932, Riech et al. 1980, Teskey and Hinckley 1981, Dell and Wallace 1983). There are, however, some exceptions to this general pattern. For example, root growth of Alaskan taiga trees had only one short growing period prior to the soil freezing in autumn (Tryon and Chapin 1983), and seedlings of *Larix decidua* Mill. exhibited only one surge of root growth during the limited growing season in the European Alps (Tranquillini 1979).

The summer depression between vernal and autumnal root growth has been correlated with moisture stress (Rogers 1939, Morrow 1949, Leshem 1965, Yaroslavtsev and Kuznetsov 1982). Merritt (1968) worked with stressed and unstressed seedlings of *Pinus resinosa* Ait. in a controlled environment and observed the bimodal (spring/autumn) pattern first identified by Resa (1878). She suggested that even though environment influences root growth intensity and timing, that the basic pattern of root growth was the expression of an identifiable 'endogenous rhythm'. By contrast, Romberger (1963 p.77) believed that "there is no reason for supposing that root growth follows an endogenous cycle, nor is there any strong evidence suggesting it." Yet, individual roots have been shown to exhibit 'endogenous seasonal rhythms' (see Wilcox 1962, Johnson-Flanagan and Owens 1985).

The objective of this research was to gain a better understanding of root physiology of *Eucalyptus pauciflora* Sieber ex Sprengel ssp. *pauciflora*

[1]Current Address: Global Forest, PO Box 3887, Main Branch, 349 Georgia Street, Vancouver, British Columbia, Canada V6B 3Z3

© 1998 by the Northwest Scientific Association. All rights reserved.

in Victoria, Australia. This study: 1) examined the relationship between soil temperature and soil moisture on monthly and seasonal root numbers of mature *E. pauciflora* ssp. *pauciflora* trees, and 2) compared the period of onset and cessation of shoot growth with that of root growth.

Materials and Methods

The Study Area

Mt Stirling in the Victorian Alps, southeastern Australia (37°07′S, 146°48′E) has an elevation of 1747 m and is classified as a steep alpine-subalpine mountain (Costin 1957). The climate is characterized by warm, dry summers and cold, wet winters. The mean maximum air temperature of January is 19°C; the mean maximum of June is -1°C. Temperature extremes of -12°C to 31°C have been recorded and frosts can occur in any month (Anon. 1992). Annual precipitation ranges from 1600 to 2000 mm yr^{-1} with a winter maximum of 200 mm $month^{-1}$ and a summer minimum of 100 mm $month^{-1}$ (Anon. 1992). Precipitation falls as snow from two prevailing weather systems; the west to northwest falls are heavier and more frequent and typically occur as blizzards and produce mostly drier snow. The south to southwest falls, on the other hand, are associated with lighter winds and snow which is typically wet and heavy.

The study site on Mt Stirling was located at 1545 m. The duration of continuous ground cover snow during the study (1992-1995) was always greater than one month per annum (Table 1) so this site was thus classified as subalpine (Costin et al. 1952). *E. pauciflora* ssp. *pauciflora* was the climatic climax species and existed as a pure stand at this site. The age of the trees as measured by increment core ranged from 99- to 182-years-old. The stand at the study site had a mean height of 9 m and a stand density of about 235 stems ha^{-1}. It would be classified as a low open forest by Specht (1970). The understory was comprised of *Oxylobium alpestre* F. Muell., *Prostanthera cuneata* Benth, and a *Poa* sp. The soil was an alpine uniform humus (Northcote 1979) with a dark loamy, sandy A horizon, 350 mm deep having a bulk density (within the top 75 mm) of 0.67 g cm^{-3}. There were no sharp boundaries between the successive horizons and one gradually merged with the next (cf. Costin et al. 1952). Numerous mountain earthworm (*Megascolex* sp.) cast filled tunnels were evident throughout the A horizon, and active *Megascolex* were observed during the winter. Floaters in the A horizon of undecomposed granitic rock accounted for a coarse fragment content of about 15% of soil volume. The pH of the soil (upper 100 mm) was 4.1 in water (mixture 4:1). The C horizon was noted by its lighter color and lack of earthworm activity. The parent material of Mt Stirling was of granitic origin. A thermohygrograph and a soil thermograph at 50 and 200 mm were kept on-site in a Stevenson's screen and maintained for the duration of the 31-month study. Environmental and physical constraints prevented continuous weather readings for July and August of each winter. The rainfall data were taken at an elevation of 1707 m from the Mt Buller weather station, which was about 6 km southwest of the Mt Stirling site.

TABLE 1. Duration of continuous snow cover at 1545 m on Mt Stirling, Victoria, Australia.

Year	Duration (weeks)
1992-93	18
1993-94	5
1994-95	14

Methods

A square plot (20 x 20 m) was delineated in November 1992. The plot had a slope of 20° with a southerly aspect. Seasonal root numbers from December 1992 to June 1995 of *E. pauciflora* were assessed from eight cores (70 mm diameter x 200 mm long) collected randomly each month at the site. There were abundant roots, with many root intercepts of *E. pauciflora* at all sampling points. Eucalypt long roots can be readily distinguished by their epidermis, root hairs, and shape of the root cap from the roots of understory species (cf. Chilvers 1972). Active root growth was determined under a stereo-microscope (x75) by examining carefully *E. pauciflora* root tips from each soil core. Root apices of 1st, 2nd, and 3rd orders were considered to be growing and only counted if they were white and abundantly supplied with root hairs (cf. Richardson 1958, Chilvers and Pryor 1965). Brown roots were assumed to be dormant and/or undergoing secondary development and were not counted. There was no evidence of root herbivory

during the study period. Ectomycorrhizal roots (as described by Chilvers and Pryor (1965)) were observed each month but not considered in this study. After each core was thoroughly examined the gravimetric soil water content was then determined. The only available access to the site during the winter snow-fall months was via cross-country skis and winter measurements included snow depths and snow densities as well as the monitoring of root numbers. In addition, one ski trip was made to the site on 1 August 1994 in between the regular sampling intervals. A hand held digital thermometer was used at 10 min intervals between 0500 and 0600 h and 1430 and 1530 h to obtain mean soil temperatures at 50 mm depth when the weather station was inoperable. These time periods were used because they represented the minimum and maximum occurrences of soil temperatures during September to June when the weather station was operational.

The live below-ground biomass of *E. pauciflora* separated from understory roots was quantified from 10 cores (70 mm diameter x 200 mm long) taken in the spring in October 1994 and again in 1995. *E. pauciflora* roots were divided into two diameter classes of <1 mm and 1- 5 mm, and their masses were obtained after oven drying at 50°C for 72 h. The roots were then ignited in a muffle furnace at 550°C for 9 h to determine the mass of mineral matter (residual ash) in the sample. Results are presented as ash-free.

Twelve *E. pauciflora* saplings or trees ranging in height from 1 to 7 m were selected from the site in March 1994 and shoot growth was measured until June of 1995. Shoot growth (length and width of buds and leaves and stem girth at dbh) was measured similarly to that described by Ashton (1975) with vernier calipers (accurate to 0.1 mm). At least three shoots were measured per sapling or tree and active growth was considered to commence when the first leaf emerged from the terminal bud. Throughout the shoot measurement period only 2 of the 36 buds measured experienced some herbivory. In those cases measurements were taken from the primary axillary bud (see Cremer 1972 for terminology).

A step-wise multiple regression was used to examine empirical relationships between growth and some environmental factors for *E. pauciflora* (see Costin 1965, Slatyer and Morrow 1977). The same method was employed in the this study using the software of StatView V4.0 to examine relations between and among root growth and environmental factors. Root numbers were considered as the dependent variable and soil temperature and soil water content as independent variables. The equation was of the form:

$$\mathbf{R}_p = b_1 (\mathbf{T}_s) + b_2(\theta_g) + b_o$$

Where:

$\mathbf{R}_p$ = the number of uninfected white roots

$\mathbf{T}_s$ = the soil temperature at 50 mm in °C

θ_g = gravimetric water content (wt/wt)

The statistical significance was determined at $P \leq 0.05$.

Results

The monthly root numbers, maximum and minimum soil temperatures at a depth of 50 mm depth, and the gravimetric water content over a 31-month period are presented in Figure 1. In general, root growth of *E. pauciflora* followed the seasonal pattern of soil temperature, increasing into summer and decreasing into winter (Figure 1B). When all of the months of the years were considered, stepwise regression showed that temperature contributed largely but soil water content relatively little to the variation in root numbers (Table 2). However, during the months of low soil water (December through March) soil water content did contribute significantly and more so than soil temperature (Table 2). Temperatures did not decline below 0.5°C at 50 mm depth during any sampling occasions (Figure 1B). Some root growth of *E. pauciflora* occurred at soil temperatures < 3°C under snow cover (Table 3) in early winter in three consecutive years (Figure 1A). A period of root dormancy of about 1 month was observed during the winter (August) of 1994 (Figure 1A and data not shown for 1 August). In September 1993 spring root growth commenced when soil temperature at 50 mm depth reached 3.5°C whereas in September 1994 it occurred when the soil temperature was 1.5°C under 550 mm of snow (Figure 1B).

There was a considerable drop in root numbers during three consecutive January's (mid-summer) followed by a rapid increase in February root growth (except in 1995) (Figure 1). Soil temperature and water content in January 1993 and 1994 did not appear to be limiting for root growth

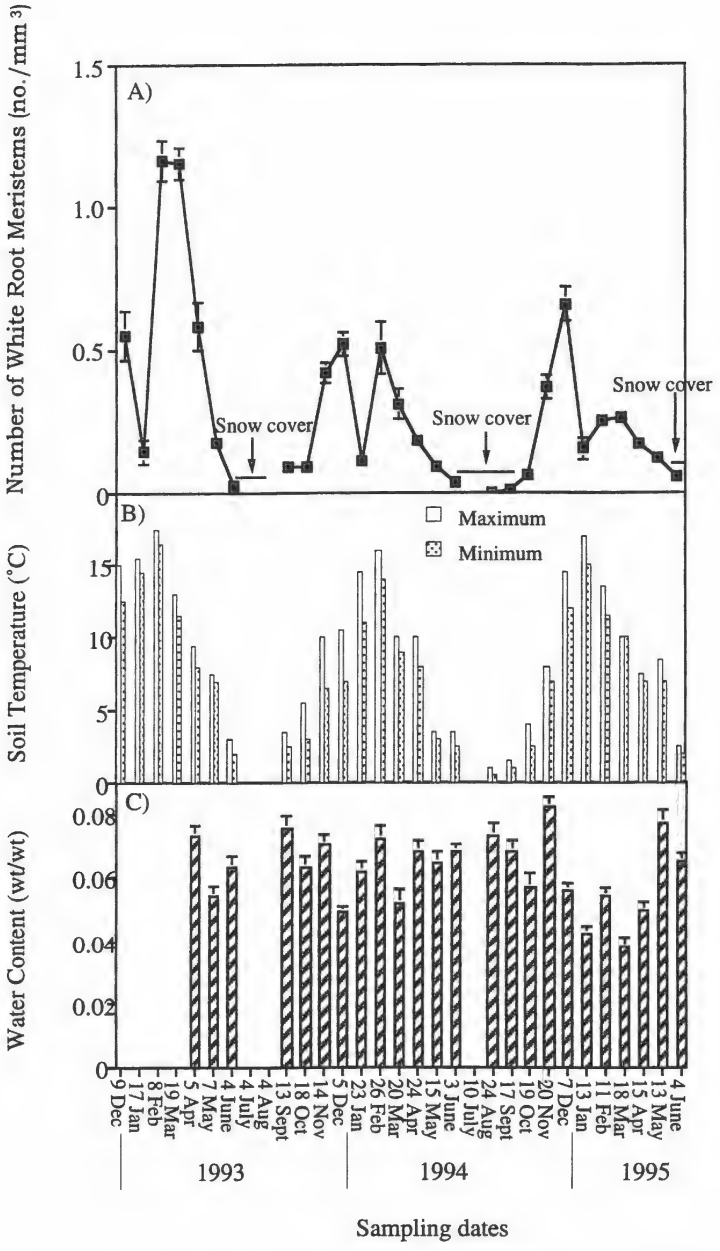


Figure 1. Monthly root numbers of *E. pauciflora* in the surface 200 mm of the mineral soil (A), maximum and minimum soil temperatures at 50 mm soil depth (B), and gravimetric water content of the surface 200 mm soil layer (C) on Mt Stirling, Victoria, Australia. Vertical bars indicate ± SE of each mean, n=8. Error bars are not shown when smaller than the symbols.

TABLE 2. Results of multiple regression analyses of root numbers as a function of soil temperature and gravimetric soil moisture content for 3 time periods—summer (Dec-Mar), other months, and all months. T_s = Soil Temperature (°C) at 50mm; θ_g = Gravimetric soil moisture content (wt/wt).

Occasion		Variable T_s	Variable θ_g	Intercept	r^2	P value
Dec-Mar	F value	24	36			
	Coeff.	1.36	438.82	-13.50	0.41	0.05
Other Months	F value	233	5			
	Coeff.	3.21	300.40	-26.11	0.43	0.01
All Months	F value	109	7			
	Coeff.	2.88	235.24	-18.86	0.46	0.01

TABLE 3. The range of snow depths and snow density at 1545 m on Mt Stirling, Victoria, Australia from 1992 to 1995. Values in parentheses are ±SE, n=8.

Sampling Date (days)	Snow Depth (m)	Snow Density (g cm^{-3})
1 Sept 1992	2.0-2.10	0.44(0.01)
13 June 1993	0.30-0.35	0.20(0.01)
23 Aug 1994	0.45-0.55	0.41(0.02)
17 Sept 1994	0.40-0.70	0.45(0.03)
4 June 1995	0.08-0.10	0.18(0.01)

(Figures 1B & C). An examination of the duration of shoot and root growth of *E. pauciflora* revealed several salient features (Figure 2). Root growth of *E. pauciflora* on Mt Stirling continued for at least 1 month after shoot growth had stopped in April 1994 and resumed at least 1 month before shoot elongation in November 1994. The root growing season extended 1 month beyond that of shoot growth in 1995. In addition, as shoot growth peaked in January of 1995 root numbers were markedly depressed, and a second maximum in root growth coincided with slowing autumn shoot growth (Figure 2).

The mean below-ground biomass of *E. pauciflora* fine roots (<5 mm diameter) in the top 200 mm of the soil in October, 1994, was 8.3 t ha^{-1} (±1.3 SE). In October, 1995, it was slightly higher at 8.9 t ha^{-1} (±1.1 SE) but not significantly so. The mineral contamination of roots on each occasion was < 5%.

Discussion

The seasonal variability in root numbers of *E. pauciflora* was related primarily to soil temperature and secondarily to soil water content. New

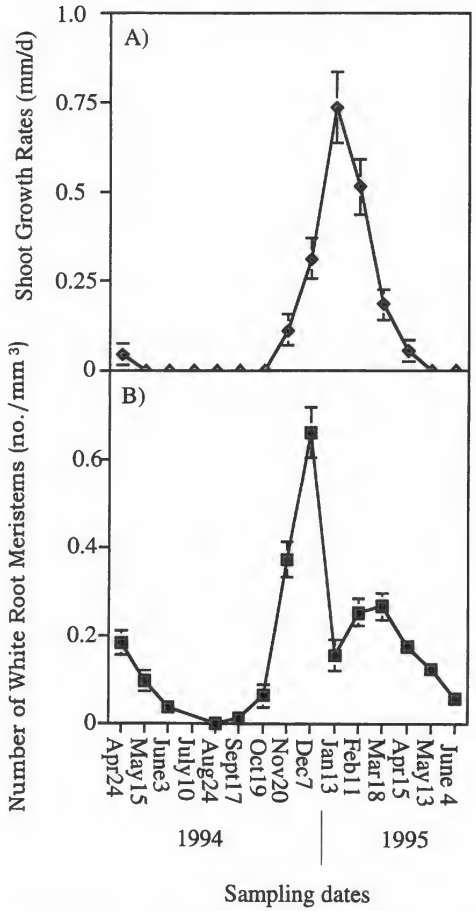


Figure 2. Shoot growth (A) and root numbers (B) of *E. pauciflora* on Mt Stirling, Victoria, Australia. Vertical bars indicate ± SE of each mean; n=8 for roots and n=36 for shoots. Error bars are not shown when smaller than the symbols.

root numbers (at both 50 and 200 mm depths) were low at low soil temperatures at the beginning and end of winter and increased with soil temperature. The occasional reduction in root numbers during summer when soil temperatures were still high may have been related to low soil water contents in some but not all instances (Figure 1, Table 2). For example, the reduction of root growth in January 1995 could have been caused by low soil moisture content from December 1994 to January 1995 experienced at the site (Figure 1C). However, the second peak in root growth in March 1995 took place at a lower soil water content and a lower soil temperature than in January 1995 (Figure 1C). Seasonal root production of *E. marginata* Donn ex Sm. within the top 50 mm was characterized by flushes of long- and short-roots in early summer (December) and later autumn (May/June) and after light summer rains (<5 mm). It was concluded that both root initiation and elongation were markedly periodic (Dell and Wallace 1983). Dell and Wallace (1983) postulated that periods of root inactivity were a result of seasonal drought conditions in the Western Australian summer, and low soil temperatures and/or hormonal levels during late winter (August). The seasonal pattern of root numbers of *E. pauciflora* was similar to that of *E. marginata* although the mid-summer drop in *E. pauciflora* root numbers was shorter and not always associated with low soil moisture. *E. pauciflora* ssp. *pauciflora* and *E. marginata* are geographically and altitudinally dissimilar yet it is interesting that both species displayed similar seasonal patterns of root growth.

At high-elevations in the Southern New Zealand Alps *Nothofagus solandri* var. *cliffortioides* (Hook. f.) Poole and *P. contorta* Dougl. also showed a similar bimodal seasonal pattern of root growth (Benecke et al. 1978). Spring root growth commenced as the soil temperature approached the 10°C soil isotherm, and autumn root growth rates declined when the soil temperature dropped below 10°C (Benecke et al. 1978). In addition, Benecke et al. (1978) recorded a drop in root production due to a mid-summer moisture stress. By contrast, *Abies amabilis* in the Cascade Mountains of Washington State, exhibited several peaks in root growth that were non-synchronous with soil temperature during the year. Root production increased sharply 2 weeks before the soil temperature warmed in the spring and declined much slower than the soil temperatures through the autumn and the winter (Keyes 1982). In the present study there was a reduction in root numbers in January 1995 without any corresponding reduction in shoot growth rates. If there was significant water stress at this time, then a reduction in shoot growth would have been expected as well. The fact that no shoot growth reduction was observed is consistent with the view that there is some internal periodicity in root growth which is independent of the external environment (cf. Teskey and Hinckley 1981), but this assumes that root herbivory can be excluded.

The duration of shoot growth of *E. pauciflora* on Mt Stirling lasted approximately 7 months which is consistent with other subalpine studies of this species (Slatyer and Morrow 1977) and less than the 7 to 9.5 months of shoot growth reported for lower elevation montane *E. regnans* F. Muell. (Ashton 1956, 1975). Growth of roots in the spring prior to shoot elongation is well documented for many Northern Hemisphere trees (Lyr and Hoffmann 1967) and was found in this study for *E. pauciflora*, with *E. regnans* (Ashton 1956), and for *E. marginata* by Dell and Wallace (1983), who, however, found root production in spring preceded shoot production by several months and that root production is summer was greatly reduced by water stress. Assimilate partitioning, as suggested for other species by Keyes (1982), may account for the increase in shoot growth and the decrease in mid-summer root numbers of *E. pauciflora.* However, other complex interactions between hormones, soil moisture and competing vegetation may also have caused this reduction. Winter root growth under a snow cover was observed on Mt Stirling and has also been recorded in North America for *A. saccharum* (Morrow 1949), *Prunus salicina* Lindl. budded on *P. cerasifera* Ehrh. (Bhar et al. 1970), and *A. amabilis* (Keyes 1982). Perhaps one outcome of continued (slow) root growth into unexploited soils in the winter is the establishment of a root-framework with a potential to produce new meristems upon renewed spring root growth. Moreover, the early spring resumption of tree root growth at low soil temperatures, in some cases under a snow cover, could provide a competitive advantage over understory root growth, and may also compensate for a mid-summer reduction in root production.

The ability to renew spring root growth under a snow cover does not appear to have been

conferred to roots of *N. solandri* var. *cliffortioides*. In this species the initiation of root growth was delayed by 2 to 3 weeks in September 1965 because of a remaining snow cover which maintained the soil temperature near 0°C (Benecke et al. 1978). Nevertheless, some root growth of *N. solandri* var. *cliffortioides* was recorded by these workers in June and mid-July 1964 (presumably not under snow cover but not stated) and they concluded that these root systems were capable of physiological activity for 9 months or more of the year. This was also found with roots of *E. pauciflora* on Mt Stirling.

Keyes (1982) found that root initiation of understory vegetation occurred 2 to 3 weeks earlier in the spring-time than that of *A. amabilis*. No white roots of understory species on Mt Stirling were observed in September 1994 under a snow cover with soil temperatures of 1.5°C (data not shown).

The causes of periodicity in root growth and the correlated growth of roots and shoots are linked to carbohydrates and source-sink relationships, water relations, and hormonal factors (Borchert 1991). Current photosynthate is required for root elongation [starch mobilization may explain root growth, which is required for bud expansion in the early spring, but current carbohydrates are required for root elongation (Wilson and Bachelard 1975, Webb 1976, van den Driessche 1987, Vapaavuori et al. 1992)]. Since root growth is associated with that of the shoot, there is a correlating influence of one on the other (Kramer and Kozlowski 1979). Water stress may provide the best explanation of correlated growth (Kramer 1983). Shoot growth may be regulated by root-limiting supply of water (Sands and Mulligan 1990). Likewise, shoot growth influences root growth by providing a source of carbon and energy (Sands and Mulligan 1990). Root growth precedes shoot growth in the spring, and the hormonal influences from the shoot (auxin) are required for shoot growth and root influences (cytokinins) also play a role (Pilet 1991). Furthermore, hydraulic conductivity also increases in the spring and improved water relations may assist spring growth (Teskey et al. 1984).

In conclusion, the seasonal variability in root numbers of mature subalpine *E. pauciflora* saplings and trees appeared to be related more to soil temperature and less to soil water content. Furthermore, evidence is presented which suggested that root periodicity in *E. pauciflora* may also be endogenous and can occur independently of the external environment.

Acknowledgements

Dr Reese Halter was the recipient of a postgraduate scholarship from Global Forest and acknowledges research grants from The University of Melbourne and the Commonwealth Scientific and Industrial Research Organisation (CSIRO), Division of Forestry, Cooperative Research Agreements. It is a pleasure to acknowledge the many stimulating discussions and contributions of Professor Roger Sands, School of Forestry, University of Canterbury, New Zealand, formerly at the School of Forestry, The University of Melbourne, Australia, and Dr David H Ashton, School of Botany, La Trobe University, Australia, formerly at the School of Botany, The University of Melbourne, Australia, throughout my doctoral studies.

Literature Cited

Anon. 1992. Information, education and resource kit. Mount Stirling alpine resort, Alpine Resorts Commission, Victoria, Australia, unpublished report.

Ashton, D.H. 1956. Studies on the autecology of *Eucalyptus regnans* F. Muell. University of Melbourne, Melbourne. Ph. D. Dissertation.

Ashton, D.H. 1975. The seasonal growth of *Eucalyptus regnans* F. Muell. Aust. J. Bot. 23:239-252.

Benecke, U., G. Baker, and I.J. McCracken 1978. Tree growth in the Craigieburn range. *In* Revegetation in the rehabilitation of mountain lands. Symp. No. 16, Forest Research Institute and New Zealand Forest Service, Christchurch. Pp.77-98.

Bhar, D.S., G.F. Mason, and R.J. Hilton 1970. *In situ* observations on plum root growth. J. Amer. Soc. Hort. Sci. 95:237-239.

Borchert, R. 1991. Growth periodicity and dormancy. *In* A. Raghavendra (ed.) Physiology of trees. John Wiley & Sons, Toronto. Pp.221-245.

Bowen, G.D. 1991. Soil temperature, root growth, and plant function. *In* Y. Waisel, A. Eshel, and U. Kafkafi (eds.) Plant roots: the hidden half. Marcel Dekker, New York. Pp.309-330.

Chilvers, G.A., and L.D. Pryor 1965. The structure of eucalypt mycorrhizas. Aust. J. Bot. 13:245-259.

Chilvers, G.A. 1972. Tree root pattern in a mixed eucalypt forest. Aust. J. Bot. 20:229-234.

Costin, A.B., E.G. Hallsworth, and M. Woof 1952. Studies in paedogenesis in New South Wales. III. The alpine humus soils. J. Soil Sci. 3:191-221.

Costin, A.B. 1957. The high mountain vegetation of Australia. Aust. J. Bot. 5:173-189.

Costin, A.B. 1965. Management opportunities in Australian high mountain catchments. *In* W.E. Sopper, and H.W. Lull (eds.) International Symp. of forest hydrology, Pergamon Press, Penn State University. Pp.565-577.

Cremer, K.W. 1972. Morphology and development of the primary and accessory buds of *Eucalyptus regnans*. Aust. J. Bot. 20:175-195.

Dell, B., and I.M. Wallace 1983. Periodicity of fine root growth in jarrah *(Eucalyptus marginata* Donn ex Sm.). Aust. J. Bot. 31:247-254.

Dengler, R.E. 1927. Theophrastus of Lesbos 372-284 BC. Der causino plantarum. Book one "Text, critical apparatus, translation and commentary", A thesis in Greek presented to the Faculty of the Graduate School, University of Pennsylvania, Philadelphia.

Duhamel du Monceau, M. 1758. La physique des arbes. Guerin and Delatour, Paris.

Goff, E.S. 1898. The resumption of root growth in spring. Wisconsin Ag. Exp. Stn. Ann. Rep. 15. Pp.220-228.

Harris, G.H. 1926. The activity of apple and filbert roots especially during the winter months. Amer. Soc. Hort. Sci. Proc. 23rd Meeting. Pp. 414-422.

Hilton, R.J. 1978. Root growth in the Guelph rhizotron. *In* A Riedacker and J. Gagnaire-Michard (eds.) Root physiology and symbiosis. International Union of Forest Research, Nancy, France. Pp.135-142.

Johnson-Flanagan, A.M., and J.N. Owens 1985. Development of white spruce *(Picea glauca)* seedling roots. Can. J. Bot. 63:456-462.

Keyes, M.R. 1982. Ecosystem development in *Abies amabilis* stands of the western Washington Cascades: root growth and its role in net primary production. University of Washington, Seattle. Ph.D. Dissertation.

Kinman, C.F. 1932. A preliminary report on root growth studies with some orchard trees. Amer. Soc. Hort Sci. Proc. 29th-30th Meetings. Pp.220-225.

Kramer, P.J., and T.T. Kozlowski 1979. Physiology of woody plants. Academic Press, Toronto.

Kramer, P.J. 1983. Water relations of plants. Academic Press, San Diego.

Kuhns, M.R., H.E. Garrett, R.O. Teskey, and T.M. Hinckley 1985. Root growth of black walnut trees related to soil temperature, soil water potential, and leaf water potential. For. Sci. 31:617-629.

Leshem, B. 1965. The annual activity of intermediary roots of Aleppo pine. For. Sci. 11:291-298.

Lyr, H., and G. Hoffmann 1967. Growth rates and growth periodicity of tree roots. *In* J.A. Romberger, and P. Mikola (eds.) International review of forest research, Academic Press, New York. Vol. 2. Pp.181-236.

Merritt, C. 1968. Effect of environment and heredity on the root-growth patterns of red pine. Ecology 49:34-40.

Morrow, R.R. 1949. Periodicity and growth of sugar maple surface layer roots on two experimental areas. Syracuse University, Syracuse. Ph.D. Dissertation.

Northcote, K.N. 1979. A factual key for the recognition of Australian soils. Rellim Technical Publications, Coffs Harbour, New South Wales, Australia.

Pilet, P.-E. 1991. Root growth and gravireaction: implications of hormones and other regulators. *In* Y. Waisel, A. Eshel, and U. Kafkafi (eds.) Plant roots: the hidden half. Marcel Dekker, New York. Pp.179-204.

Reich, P.B, R.O. Teskey, P.S. Johnson, and T.M. Hinckley 1980. Periodic root and shoot growth in oak. For. Sci. 26:590-598.

Resa, F. 1878. Untersuchungen über die Periode der Wurzelbildung insbesondere bei den Holzgewächsen. Forstl. Bl. 15:321-331.

Rogers, W.S. 1939. Root studies. VIII. Apple root growth in relation to rootstock, soil, seasonal and climatic factors. J. Pom. HortSci. 17:99-142.

Romberger, J.A. 1963. Meristems, growth, and development in woody plants. USDA Tech. Bull, Washington, DC. No. 1293.

Ross, C.B. 1932. Root development of western conifers. M.Sc. Thesis, Univ. of Washington, Seattle.

Sands, R., and D.R. Mulligan 1990. Water and nutrient dynamics and tree growth. For. Ecol. Manage. 30:91-111.

Slatyer, R.O., and P.A. Morrow 1977. Altitudinal variation on the photosynthetic characteristics of snow gum, *Eucalyptus pauciflora* Sieb ex Spreng. I. Seasonal changes under field conditions in the snowy mountain area of south-eastern Australia. Aust. J. Bot. 25:1-20.

Specht, R.L. 1970. Vegetation. *In* G.W. Leeper (ed.) The Australian environment, CSIRO and Melbourne University Press, Melbourne. Pp.44-67.

Teskey, R.O., and T.M. Hinckley 1981. Influence of temperature and water potential on root growth of white oak. Physiol. Plant. 52:363-369.

Teskey, R.O., T.M. Hinckley, and C.C. Grier 1984. Temperature-induced change in the water relation of *Abies amabilis* (Dougl.) Forbes. Plant Physiol. 74:77-80.

Tranquillini, W. 1979. Physiological ecology of the alpine timberline: tree existence at high altitudes with special reference to the European Alps. Springer-Verlag, Berlin.

Tryon, P.R., and F.S. Chapin 1983. Temperature control over root growth and root biomass in taiga forest trees. Can J. For. Res. 13:827-833.

van den Driessche, R. 1987. Importance of current available photosynthate to new root growth in planted conifer seedlings. Can. J. For. Res. 17:776-782.

Vapaavuori, E.M., R. Rikala, and A. Ryyppö 1992. Effects of root temperature on growth and photosynthesis on conifer seedlings during shoot elongation. Tree Physiol. 10:217-230.

Wardle, P. 1968. Engelmann spruce (*Picea engelmannii* Engel.) at its upper limits in the front range, Colorado. Ecology 49:483-495.

Webb, D.P. 1976. Root growth in *Acer saccharum* Marsh. seedlings: effects of light intensity and photoperiod on root elongation rates. Bot. Gaz. 137:211-217.

Wilcox, H. 1962. Growth studies of the roots of incense cedar, *Libocedrus decurrens*. II. Morphological features of the root system and growth behaviour. Am. J. Bot. 49:237-245.

Wilson, B.F., and E.P. Bachelard 1975. Effects of girdling and defoliation on root activity and survival of *Eucalyptus regnans* and *E. viminalis* seedlings. Aust. J. Pl. Physiol. 2:197-206.

Woodroof, J.G., and N.C. Woodroof 1934. Pecan root growth and development. J. Ag. Res. 49:511-530.

Yaroslavtsev, G.D., and S.I. Kuznetsov 1982. Seasonal changes of growth activities of cedar-roots. Nitiski Bot. Garden, No.48. Pp.39-42.

Received 7 March 1998
Accepted for publication 20 October 1998

John Duff Bailey, School of Forestry, Northern Arizona University, Flagstaff, Arizona 86011-5018

and

Leon H. Liegel, USDA Forest Service, Pacific Northwest Research Station, Corvallis, Oregon 97331

Pacific Yew (*Taxus brevifolia* Nutt.) Growth and Site Factors in Western Oregon

Abstract

Conservation biologists in the Pacific Northwest have recently turned their attention to Pacific yew (*Taxus brevifolia* Nutt.), given past harvest of this species for taxol and the fragmentation of late-successional forested landscapes. Understanding yew growth and reproduction patterns is important given interest in the long-term viability of yew populations and important contributions this species makes to stand structure. Our research, based on data from 11 intensively measured 2-ha plots, confirms and quantifies some early qualitative observations of yew tree size and age distributions in three forested subregions of western Oregon. These distributions show a general lack of regeneration in the last century, which should be of some concern to land managers given Pacific yew's contribution to late-successional stand structure. Although correlations between size measurements, for example between diameter and height, are strong (coefficients > 0.61 across all plots) and consistently positive, correlations between size and site variables (e.g., aspect) are weaker (coefficients < 0.41 across all plots) and inconsistent. Most plots demonstrated a weak but consistent relationship between size and age, and yew tree size and age distributions were relatively consistent within subregions. However, there were substantial differences in diameter growth rates among subregions.

Introduction

Pacific yew is a relatively slow-growing, coniferous tree species found in the understory of undisturbed forests from northern California to central British Columbia, and inland to Idaho (Bolsinger and Jaramillo 1990). Through the early 1990s, yew bark was the only approved source of taxol, a drug used to treat several forms of cancerous tumors (Wani et al. 1971, Rowinsky et al. 1990). Demands for taxol dramatically accelerated the harvest - both legal and illegal - of yew trees growing on private and federal forests in Oregon, Washington, and California. This acceleration threatened the distribution and demographics of the species at local and regional levels, drawing the attention of scientists, federal land managers, and conservationists. Advances in taxol synthesis allowed the Bristol-Myers-Squibb Corporation to stop purchasing Pacific yew bark from federal lands in 1992. However, past and current logging practices that increase fragmentation of large late-successional forested landscapes still focus attention on the conservation biology of Taxus and other genera growing in Pacific Northwest forests (Spies et al. 1994; Busing et al. 1995).

Yew trees are extremely shade tolerant and occur as scattered individuals or clumps across diverse landscapes, being most abundant in the understory of older forests lacking recent large-scale disturbance (Busing et al. 1995). Though undocumented, yew tree growth in undisturbed forests likely follows a sigmoidal curve or related growth pattern over time. Yew trees survive and their radial growth increases following partial overstory removal associated with thinning or shelterwood treatments (Bailey and Liegel 1997). However, yew foliage is harmed by sun, wind, or cold exposure following heavy canopy removal associated with clearcut logging (Bolsinger and Jaramillo 1990; Busing et al. 1995). Vegetative reproduction from stumps is common following cutting; yew can sprout from damaged or buried stems and branches even if most of the tree is killed (Bolsinger and Jaramillo 1990; Minore and Weatherly 1996). However, clearcut logging and site burning after harvest severely limit regeneration (Busing et al. 1995). These limits on regeneration and the cutting of older individuals in the population have had major impacts on landscape demographics.

Information on specific site and stand factors that influence Pacific yew populations is limited; thus, it is difficult to build models that predict tree and regeneration locations within forests or to identify optimal environmental conditions for culturing yew for understory structure in managed stands. Busing and Spies (1995) used long-term

© 1998 by the Northwest Scientific Association. All rights reserved.

data sets to develop a preliminary stand-level model of Pacific yew population dynamics, and they called for additional models to characterize growth dynamics and autecology of yew across diverse landscapes. Our intent in this paper is to further the understanding of yew size and age structure and potential environmental factors regulating yew populations in western Oregon.

We present results from a research effort designed to identify site and stand factors associated with yew populations. We characterized the surrounding landscape, over- and understory vegetation, site history, and reproduction in late-successional Douglas-fir stands. We also quantitatively and qualitatively compared sizes and ages of yew trees both within and across western Oregon subregions. Such information provides a basis for constructing sound hypotheses about the spatial arrangement of yew within landscapes and for predicting yew size and age structure for specific environmental conditions.

Methods and Materials

Study plots were located in three physiographic subregions of western Oregon Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) forests (Figure 1): Central Cascades (4 plots), Willamette Valley (4 plots), and Coast Range (3 plots). These are referred to as Cascade, Valley, or Coast in the rest of the text. All 11 sites had characteristics typically associated with late-successional Douglas-fir stands: large living trees >200 years old, large snags, and a multi-storied canopy (Franklin and Spies 1991). Three sites had a recent history of partial harvesting (Table 1). Two-ha square plots, 142 m per side, were established in the first 3-4 stands located per subregion in which preliminary reconnaissance indicated the presence of more than 10 yew trees/ha over a broad area (a moderate-to-high density). Plots had randomly located corners, referenced to the stand entry point. For each plot, we mapped individual tree location by diameter class for all yews with a diameter at breast height (DBH) of at least 7.5 cm. We also surveyed four 10-m fixed-radius subplots within each plot to characterize over- and understory tree composition and density in the 2 hectares (Table 1).

Within each plot, we randomly selected (proportionally to stand diameter distribution) approximately 20 yew trees for sampling. For each selected tree, we measured the site and tree variables listed in Table 2. Trees were defined as originating from a single stem at ground level; Pacific yew typically forks one or more times below breast height. Diameter at breast height was recorded for the largest fork in these cases. All measurement techniques were consistent with both the USDA Forest Service and USDI Bureau of Land Management Yew Inventory procedures (USDI Bureau of Land Management 1992). A portable data recorder was used for data collection and handling. Data were downloaded to a personal computer for analysis. Aspect was sine-converted.

From all sample trees, we collected four increment cores just above the stem collar (ground level), one in each cardinal direction. Cores were stored in paper straws for transport and were later mounted and sanded following procedures described by Swetnam et al. (1985). Cores were aged using a binocular microscope by multiple readers to increase accuracy. Readability of a tree's four cores often varied considerably, so tree age estimates were based on the highest quality cores. Cores were not cross-dated, and incremental growth was measured on only two sites (Bailey and Liegel 1997). Average radial growth over the life of the tree was calculated from age and diameter.

Data were checked for consistency using regressions of known relationships (e.g., collar diameter against diameter at 1.3 m, and total height against peelable height). One data point out of approximately 8000 was excluded after this validation procedure. For each plot, we used SAS to graph and regress all variable pairs showing correlation coefficients ≥0.3 and meeting normality assumptions (SAS institute, Inc. 1988). Trees and subplots were randomly located within 2-ha plots. However, because plot arrangement was not random either within or across regions, quantitative intra- and inter-regional analyses of these relationships were not performed. We used plot averages to qualitatively examine several variable relationship changes within and across regions. Plot means based on the sample tree readings were calculated for the tree growth and site variables listed in Table 2; stand-level data in Table 2 were also used. This aggregated data set with 11 nonrandom observations was examined graphically. Finally, for some analyses we attempted to reduce variation in the data set by selectively excluding certain classes of trees (e.g., the largest or smallest, damaged, or multiple-stem trees).

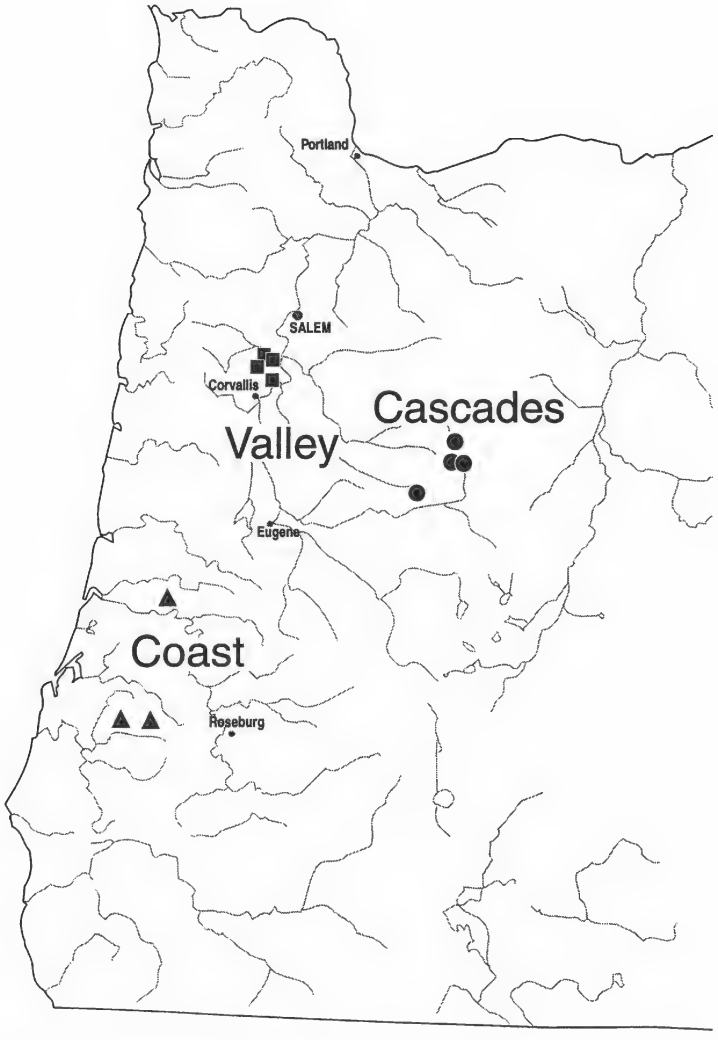


Figure 1. Study site locations in three physiographic subregions of western Oregon: western Willamette Valley (4 plots); Central Cascades (4 plots); and Coast Range (3 plots).

The intent was to improve goodness-of-fit estimates, although this data-filtering typically provided only marginal improvements.

Results and Discussion

Tree Distributions and Characteristics

Field mapping in 11 2-ha plots in late-successional western Oregon Douglas-fir forests with 15-161 Pacific yew per hectare confirmed two previous findings:

1) Pacific yew typically grows as scattered individuals or clusters within stands, supporting Bolsinger and Jaramillo (1990) and Busing et al. (1995).

2) The species primarily occurs in the understory of undisturbed stands without evidence of recent fire or other major disturbance like clearcut

TABLE 1. Site descriptions for 2-ha study plots of Pacific yew.

Region and plot	T-R-S[a]	Mean elev. (m)	Mean slope (%)	Primary aspect	Total trees/ha	Mean canopy density (%)	# yew/ha	# yew measured	Historical notes
Western Willamette *Valley*[b]									partially
1	10S-5W-16	180	42	–[c]	408	87	30	22	harvested c. 1900
2	11S-5W-7	230	56	W	323	85	30	21	
3	10S-5W-22	250	65	N	262	87	35	18	
4	11S-5W-3	230	38	W	476	92	40	22	
Central *Cascades*[b]									
5	13S-6E-36	990	25	E	228	35	72	23	thinned 1978
6	13S-6E-36	980	25	E	518	70	116	21	
7	13S-6E-25	960	25	NE	280	45	133	22	thinned 1978
8	16S-4E-25	850	45	W	289	73	98	22	
Coast[b] Range									
9	26S-9W-21	460	90	NE	185	68	17	20	
10	21S-9W-21	240	76	–[c]	271	86	15	21	
11	27S-9W-24	910	44	SE	482	73	161	18	

[a]Township, Range, and Section location.
[b]Italicized words used throughout text to identify regions.
[c]Complex terrain with no dominant aspect.

harvesting, supporting Busing et al. (1995). Recent inventory efforts by the USDA Forest Service and BLM place an actual percentage occurrence in various forest types.

In addition, we qualitatively observed that:

1) Within the Valley and Coast subregions, Pacific yew was more common on steeper slopes than on ridges, benches, or valley bottoms.

2) In all plots, Pacific yew was associated with the understory shrub species sword fern (Polystichum munitum [Kaulf.] Presl) and dwarf Oregon grape (*Berberis nervosa* Pursh).

3) Across all sites, Pacific yew seedlings were rare in these undisturbed forests, accounting for <5% of total observed regeneration, although vegetative reproduction from layering and/or stem and stump sprouts on damaged trees was common.

4) Yew growth form was quite variable across all the study plots. In 9 of the 11 plots, at least half of the sample trees had forked or multiple stems before a 3-cm diameter top (Table 3).

5) The stems of 2-5% of sampled trees were fused. Cores extracted from three single-stem trees conclusively showed two piths, and in 15 other cases multiple piths were suspected (Table 3).

6) Nearly 100% of trees in the oldest age range and largest size range sampled had pockets of rot; in >50% of the cases, they also had hollow centers.

Yew Size and Age Distributions

The distribution of collar diameters in these Pacific yew populations shows a general reverse-J pattern, particularly in Cascade plots (Figure 2). Though constructed from only the approximately 20 trees per plot, this distribution reflects that of the entire plots, since our sub-sampling was proportional across diameter classes. Age structure for these same stems, however, shows more of a broad bell-shaped, even-aged distribution. Plots were very similar within subregions; the individual plots shown are the best representatives of their subregions (Figure 2). The absence of a large number of individuals in the 10-cm size class and

TABLE 2. Yew tree site, tree growth, and stand variables and measurement techniques used in the field.

	Variable	Measurement technique
Yew tree site	Regeneration method	0 = none; 1 = stump sprout; 2 = stem sprout; 3 = seedling; 4 = unknown
	Canopy density (±4%)	Average of measurements at 4 cardinal directions at edge of yew canopy, with optical densiometer
	Slope (±1%)	Under yew canopy, with clinometer
	Slope position	0 = ridge top or bench; 1 = upper slope; 2 = side slope; 3 = bottom slope; 4 = floodplain
	Aspect (±1°)	At yew stem base, with compass
Yew tree growth		
	Diameter (±0.1 cm)	At stem collar and at breast height, with diameter tape
	Height (±0.1 m)	Total, and peelable (3-cm diameter top, with Relaskop
		Live crown (lowest live branch), with tape or Relaskop
	Live crown ratio	Calculated
	# peelable branches	Live branches >3 cm. diameter
	Crown width (± 0.1 m)	Average of measurements at 4 cardinal directions tape
	Fruiting	0 = none; 1 = present
	Damage to tree	0 = none; 1 = broken top; 2 = leaning; 3 = scarring 4 = essentially dead
	Growth form	0 = columnar; 1 = fork; 2 = multiple stems
	# epicormic sprouts	0 = none; 1 = 1–10; 2 = 11–30; 3 = >30
Stand		
	Total basal area/ha	Projected from tally over 4 fixed-radius subplots
	Total trees/ha	Projected from tally over 4 subplots
	Yew basal area/ha	Projected from tally over 4 subplots
	Yew trees/ha	Averaged from tally over 2 ha

TABLE 3. Summary of stem form, rot pockets, and possible and demonstrated fused stems of sample yew trees.

		Number of trees					
Plot #	Total # yew sampled	Single stems	Forked stems	Multi-stems	Rotten pockets	Possib. fused	Demon. fused
1	22	8	7	7	6	0	0
2	21	15	3	3	13	3	1
3	18	8	1	9	2	2	1
4	22	8	1	13	7	3	0
5	23	11	6	6	9	0	0
6	21	9	4	8	9	1	0
7	22	10	2	10	7	2	0
8	22	14	1	5	17	1	0
9	20	11	0	9	8	0	0
10	21	9	3	9	6	3	0
11	18	7	2	9	7[a]	0[a]	1[a]

[a] Figure based on observation of 16 trees, not 18 trees.

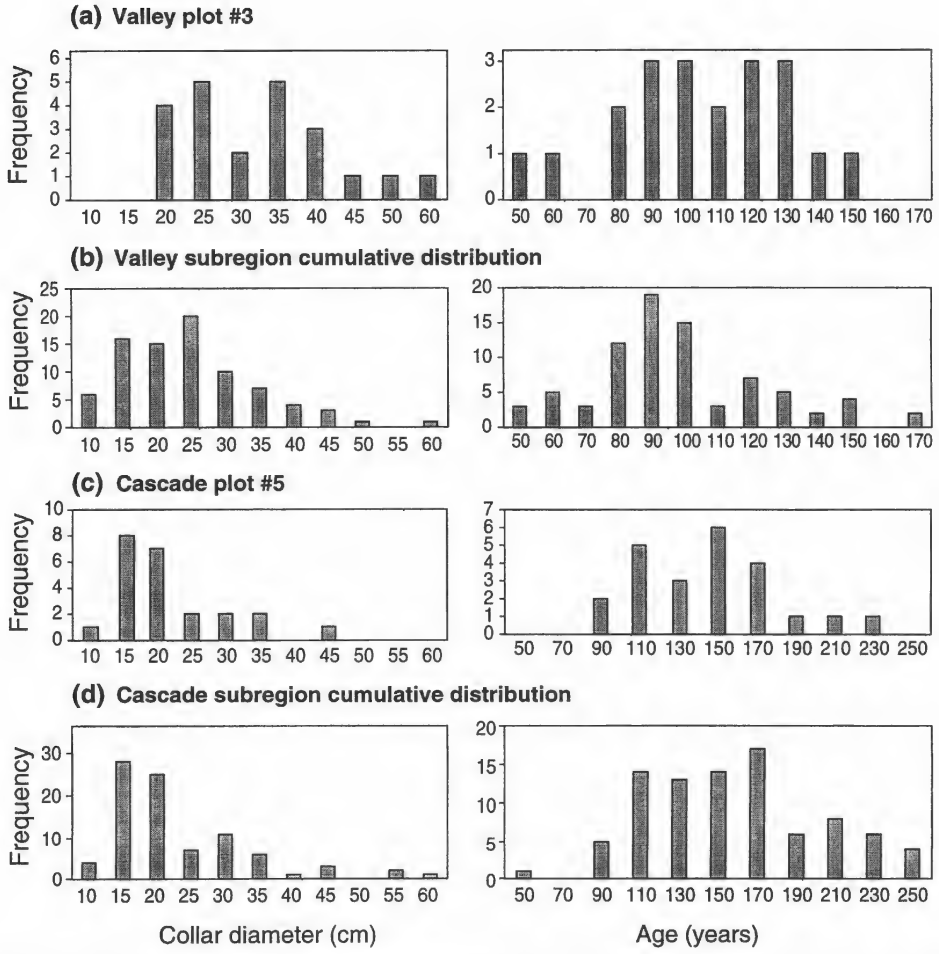


Figure 2. Collar diameter distribution and age distribution for Valley (a and b) and Cascade (c and d) plots. Cumulative distributions were constructed from >20 sampled trees per plot and 4 plots per subregion. Note the difference in age classes between the two subregions.

in age classes <100 yr demonstrates a substantial lag in yew regeneration (sprouts and/or seedlings) in the last century. This lack of smaller, younger yew trees extends well beyond our 7.5-cm minimum diameter for sampling to the general lack of reproduction noted above.

Given the difficulty of determining ages of large trees from cores (i.e., because of rotten and hollow centers), we were particularly interested in determining whether age could be predicted from collar diameter. Few plots demonstrated a strong relationship between collar diameter and age, however. Regression R^2s ranged from 0.15 to 0.75 with a median of 0.48 (average = 0.51). The maximum and minimum R^2 cases (plots) appear in Figure 3. Restricting analyses to data either for undamaged single-stem trees or for a narrower age band (80-120 yr) did not improve the collar diameter-to-age relationship.

Correlations within 2-ha Plots

Correlations between tree size variables (e.g., stem collar diameter, height, and crown variables) were consistently positive on all plots (Table 4). We

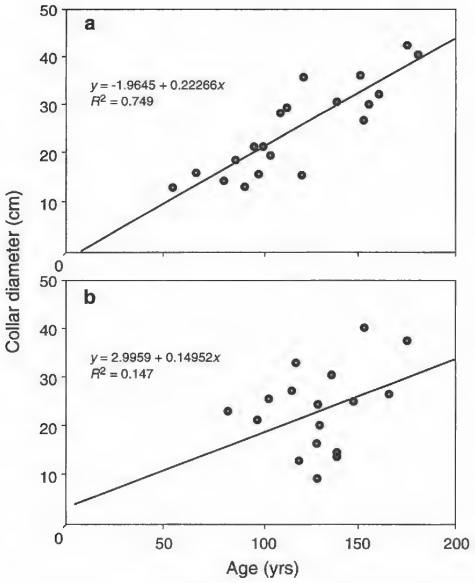


Figure 3. Yew age vs. root collar diameter in plot with (a) best R^2 (Valley plot #2) and (b) worst R^2 (Coast plot #11).

used collar height and breast height diameter even though some variability is introduced into DBH by multiple stems (Table 3). The plot 3 results shown in Figure 4 were typical for most variable pairs studied across all plots - that is, regressions demonstrated significant slopes, insignificant intercepts, and R^2s >0.6. However, correlations between site variables and tree measurements were not strong or consistent (Table 4), nor were fruiting data, given the preponderance of zeros in the data set. Likewise, correlations between tree size measurements and average radial growth were not consistent (linear or non-linear); a more complete data set supplemented with dendrochronological analysis of incremental growth is needed to determine whether yew growth follows a sigmoidal curve. Such an analysis is not possible with these data, nor is the calculation of basal area increment.

Filtering the data set for specific tree ages, sizes, and growth forms consistently improved correlations and regressions among tree variables. For example, the correlation between collar diameter and number of branches on plot 1 improved from 0.73 (based on all 22 sample trees) to 0.85 when examining only the 13 sample trees that were between 80 and 120 yr old. The correlation coefficient likewise improved to 0.93 when examining only the 6 trees with no damage and a single-stem growth form.

Ability to predict tree characteristics from site variables (e.g., slope or canopy density) was not promising; regression R^2s based on 20 trees were

TABLE 4. Correlation coefficients for pairs of yew tree size, age, incremental growth, and site variables across 11 sites.

	Valley				Cascades				Coast		
Site #:	1	2	3	4	5	6	7	8	9	10	11
Diameter (at 1.3 m) vs. total height	0.75	0.76	0.69	0.90	0.85	0.72	0.68	0.85	0.61	0.75	0.69
Collar diameter vs. crown width	0.36	0.62	0.87	0.83	0.87	0.79	0.82	0.86	0.75	0.83	0.89
Crown width vs. # of branches	0.58	0.80	0.72	0.88	0.80	0.94	0.82	0.93	0.78	0.67	0.82
Tree age vs. collar diameter	0.66	0.87	0.68	0.67	0.85	0.79	0.69	0.70	0.52	0.85	0.38
Average radial growth vs. canopy density	-0.39	-0.13	-0.22	0.18	0.08	0.06	0.00	0.08	-0.39	-0.04	-0.29
Slope vs. diameter at 1.3 m	-0.13	0.07	-0.14	-0.08	-0.20	-0.01	0.02	-0.16	0.38	0.34	-0.39
Slope vs. incremental growth	-0.22	0.25	0.00	-0.23	-0.36	-0.22	-0.11	-0.07	0.13	0.41	0.31
Sine(aspect) vs. total height	-0.02	0.22	0.09	0.02	-0.07	-0.06	0.03	0.17	-0.13	0.14	0.14
Canopy density vs. collar diameter	-0.24	-0.61	-0.32	-0.08	0.03	0.14	0.31	0.01	-0.25	0.07	-0.57

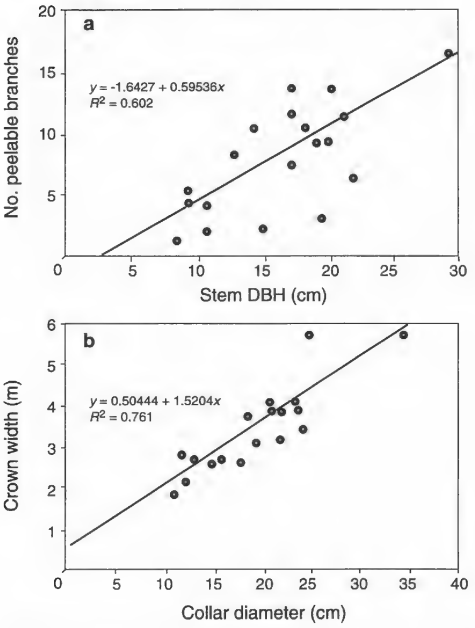


Figure 4. Relationships between pairs of yew tree growth variables in Valley plot #3: number of peelable branches vs. stem DBH (a) and crown width vs. stem collar diameter (b).

mostly <0.41. Based on Bailey and Liegel (1997), we expected canopy density to be a major correlate, but it was not. Multiple regression of site variables against tree characteristics did not significantly improve any of these correlations. Aggregating data by region also failed to improve predictive capabilities, even though significant regressions were demonstrated (e.g., with slope and aspect) based on the larger samples. Unmeasured variables, perhaps stand history attributes such as time since or distance from some disturbance, evidently have significant effects on yew growth.

Similarities among Plots, within the Same Subregion

Stand conditions and yew tree densities, sizes, and ages were most similar among Valley plots. Differences in these characteristics were larger among Cascade plots, likely due to their more diverse histories; two plots had been thinned 14 yr prior to our study. For example, average canopy density for the Cascade plots ranged from 35 to 73%, whereas canopy density of the Valley plots was 85-92%. Average canopy density for Coast plots was between these two. Within each subregion, regression patterns between pairs of tree variables and between tree and site variables typically were consistent among all plots (i.e., positive relationships on any one plot were typically positive on all plots). The statistical significance of these regressions differed among plots, however.

Similarities Across Subregions

Yew stem age ranges varied markedly across subregions (Figure 2). In Valley plots, for trees from 8.3 to 36.6 cm DBH, and readable ages ranged from 45 to 170 yr. The largest tree was 60 cm DBH; its age was estimated to be 230 yr. In the Cascade and Coast plots, trees with diameters similar to those in Valley plots (9.5-38.5 cm DBH) ranged in readable age from 80 to 260 yr, much older than those in Valley plots. The two largest trees (50.5 and 66.0 cm DBH) with rotten centers were estimated to be 350 and 400 yr. Average radial growth rates, the accumulation of diameter with time, therefore differed between Valley and Cascade plots using regressions between collar diameter and age (Figure 5). The intercepts of all eight plot lines (shown as thin lines) are not significantly different from zero; aggregated data are shown by the broad line. The regression lines for Coast plots fall between these groups, being more similar to Cascade plots and slightly above them; however, because they are not significantly different from either the Cascade or the Valley lines, we did not include them in Figure 5. Of note, Valley plot #4 and Cascade plot #8 were

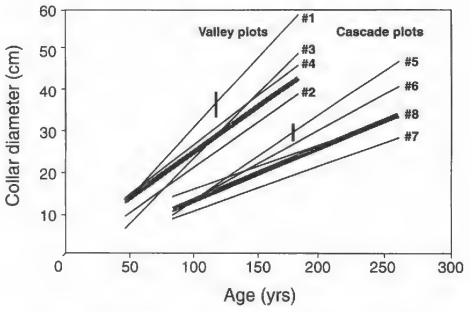


Figure 5. Regression lines for stem collar diameter vs. tree age for Valley and Cascade plots, and aggregated data regression lines (bold) for the two regions. Vertical bars on plots 1 and 5 regression lines show one standard error at mean age.

similar in all respects except for age. The direction (positive or negative) and strength of other relationships among tree variables (e.g., between collar diameter and crown width) were largely consistent among all 11 plots, with differences within any single subregion as great as those between subregions.

Stand Averages

Figure 6 shows two examples of stand averages, across all three subregions, for tree and site variables showing the strongest correlations within plots. These graphs do not prove the existence of biological relationships because these illustrated trends could be unique to the 11 plots we selected, but they nonetheless serve as hypotheses for further exploration of established correlations. Across 11 sites, yew crown width tended to increase as overstory canopy density increased (Figure 6a). Other shade-tolerant species, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and bigleaf maple (*Acer macrophyllum* Pursh), can show such characteristic changes in form with increasing shade (Franklin and Dyrness 1984). Crown width also increased as slope increased (Figure 6b). Both these results may only reflect the fact that Coast and Valley plots, which had the largest crowns, were also located on sites with denser canopies and steeper slopes.

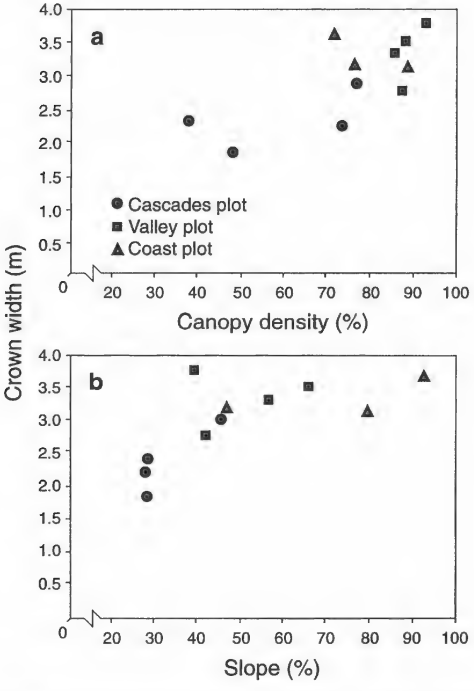


Figure 6. Tree characteristic vs. site variables for study plots: crown width vs. stand canopy density (a); and crown width vs. percent slope (b).

Conclusions

The reverse-J stem diameter distribution seen in these Pacific yew populations, in the understory of late-successional Douglas-fir forests where they are most common, suggest continual regeneration in the manner of uneven-aged populations. However, age distributions for the same stands show a dominant pulse of regeneration more than 100 years ago, resulting in a distribution more typically associated with even-aged populations with scattered older individuals. Regeneration, almost exclusively in the form of sprouts, has been low in the last century and may be explained by a reduction in low-intensity fire disturbances (which would lead to yew sprouting and/or seedbed creation), increases in seed predation and ungulate browse of young seedlings, or other changes in these forests following Euro-American settlement. This low level of recent regeneration accentuates (or perhaps creates) a bell-shaped age distribution. Additional field research specifically on Pacific yew regeneration processes will be needed to resolve this inconsistency between the expected reproductive behavior of such a shade-tolerant species (i.e., a reverse-J distribution) and the observed pattern. Other tolerant species like western hemlock reproduce more readily in the shade of an older Douglas-fir overstory.

These data also demonstrate substantial variability in yew growth trajectories among subregions, as seen in Figures 2 and 5. Yew trees are younger and grow significantly more quickly in Valley plots than in Cascade plots, although the reason for this accelerated radial growth is unclear. Valley sites were at lower elevations on average, but elevation was not significantly correlated with size or age. Valley sites had the highest overstory canopy coverage on average, but increased shading should have resulted in reduced radial growth.

We entered this study with particular interest in the relationship between overstory canopy and yew reproduction and growth rates within and

among sites. Bailey and Liegel (1997) and D. Minore (pers. comm.) have suggested that yew trees, like western hemlock (Packee 1990) and bigleaf maple (Minore and Zasada 1990), grow faster or 'release' with increased light availability. Sampling along a more extensive range of stand conditions will be necessary to improve our information on this issue.

Finally, the relationships between stand characteristics and yew reproduction, survival, and growth remain largely unquantified. The stand and site variables we measured proved to be only marginally related to yew tree variables within and among our intensive plots. Percent slope and overstory density within most sites showed the best predictive capabilities, but correlation coefficients were < 0.41. Figure 6, depicting averages for plots, shows no better relationship. The lack of correlation between stand characteristics and yew characteristics suggests the strong influences of other, unsampled factors associated with soil and/or microsite variability. Understory species are sensitive to relatively small changes in light levels, available soil moisture and nutrients, and mycorrhizal associations. In addition, chance events in a stand's history (e.g., windfall or animal damage) may no longer be in evidence but may have had a large effect on yew growth or structure. We found variation among stands therefore to be high, and planning by forest managers should acknowledge this stand-to-stand variability in addition to regional variability and age structure issues raised by these plots.

Acknowledgements

Thanks to Bristol-Myers-Squibb Corporation and the USDA Forest Service for their financial support. We extend special thanks to Don Minore, Richard Busing, Pete Owston, and John Tappeiner for reviewing earlier drafts of this paper. This is Paper 3155 of the Forest Research Laboratory, Oregon State University, Corvallis.

Literature Cited

Bailey, J. D., and L. H. Liegel. 1997. Response of Pacific yew (Taxus brevifolia) to partial removal of the overstory. West. J. Appl. For. 12:41-43.

Bolsinger, C. L., and A. Jaramillo. 1990. Taxus brevifolia Nutt. Pacific yew. *In* R. M. Burns and B. H. Honkala (tech. coords.) Silvics of North America, Volume 1, Conifers. USDA For. Serv. Agric. Handb. No. 654. Washington, D.C. Pp. 573-579.

Busing, R. T., C. B. Halpern, and T. A. Spies. 1995. Ecology of Pacific yew (*Taxus brevifolia*) in western Oregon and Washington. Conserv. Biol. 9:1199-1207.

Busing, R. T ., and T. A. Spies. 1995. Modeling the population dynamics of Pacific yew. USDA For. Serv. Res. Note PNW-RN-515. Pac. Northw. Res. Sta., Portland, Oregon. 13 p.

Franklin, J. F., and C. T. Dyrness. 1988. Natural Vegetation of Oregon and Washington. Oregon State University Press. Corvallis, Oregon.

Franklin, J. F., and T. A. Spies. 1991. Composition, function, and structure of old-growth Douglas-fir forests. *In* Wildlife and Vegetation of Unmanaged Douglas-fir Forests. USDA For. Serv. Tech. Rep. PNW-GTR-285. Pac. Northw. Res. Sta., Portland, Oregon. Pp. 71-82.

Minore, D., and H. G. Weatherly. 1996. Stump sprouting of Pacific yew. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-378. Pac. Northw. Res. Sta. Portland, Oregon. 6p.

Received 7 March 1998
Accepted for publication 27 October 1998

Minore, D., and J. C. Zasada. 1990. Bigleaf Maple. *In* Silvics of North America, Vol. 2. Hardwoods. USDA Agricultural Handbook 654. Washington, D.C. Pp. 33-40.

Packee, E. C. 1990. Western Hemlock. *In* Silvics of North America, Vol. 1. Conifers. USDA Agricultural Handbook 654. Washington, D.C. Pp. 613-622.

Rowinsky, E. K., L. A. Cazenave, and R. C. Donehower. 1990. Taxol: a novel investigational antimicrotubule agent. J. Natl. Cancer Inst. 82:1247-1259.

SAS Institute, Inc. 1988. SAS/STAT User's Guide, Release 6.03 Edition. SAS Institute, Inc., Cary, North Carolina.

Spies, T. A., W. J. Ripple, and G. A. Bradshaw. 1994. Dynamics and pattern of a managed coniferous forest landscape in Oregon. Ecol. Appl. 4:555-568.

Swetnam, T. W., M. A. Thompson, and E. K. Sutherland. 1985. Using dendrochronology to measure radial growth of defoliated trees. USDA For. Serv. Agric. Handb. No. 639. Washington, D.C. 39 p.

USDI Bureau of Land Management. 1992. Pacific yew inventory field instructions for western Oregon. USDI Bureau of Land Management, Oregon State Office, Portland, Oregon.

Wani, M. C., H. L. Taylor, and M. E. Wall. 1971. Plant antitumor agents. VI. The isolation and structure of taxol, a novel antileukemic and antitumor agent from Taxus brevifolia. J. Am. Chem. Soc. 93:2325-2327.

Douglas M. Gomez[1] and **Robert G. Anthony,** Oregon Cooperative Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331, U.S.A

Small Mammal Abundance in Riparian and Upland Areas of Five Seral Stages in Western Oregon

Abstract

We compared species composition and relative abundance of small mammals between riparian and upland habitats among five seral stages in the Coast Range of Western Oregon to determine the significance of these areas to different species. Riparian- and upland-associated species were identified based on capture frequencies from pitfall trapping. Species richness was similar between stream and upland habitats and among the five seral stages. However, there were significant differences in the abundances of nine small mammal species among seral stages. Total captures were highest in deciduous stands and progressively lower from shrub to old-growth coniferous forests. *Neurotrichus gibbsii*, *Sorex bendirii*, *Sorex pacificus*, *Microtus longicaudus*, *Microtus townsendii*, *Phenacomys albipes*, and *Zapus trinotatus* were captured in significantly higher numbers in riparian than in upland habitats. *S. pacificus* and *M. longicaudus* should be considered riparian associated species; *S. bendirii* should be considered an obligate species of riparian habitat. In contrast, *Clethrionomys californicus* showed a strong association with upland habitat. Our results indicate that small (second- third- and fourth-order) riparian systems and adjacent upland areas provide important habitat for small mammals on the Oregon Coast Ranges. Conservation plans of these riparian systems should consider these species as important components of these ecosystems.

Introduction

Riparian areas are known as some of the most productive and diverse habitats available to wildlife (Thomas et al. 1979, Oakley et al. 1985). Kauffman (1988) suggested riparian habitats may be used by large numbers of wildlife species, and play a significant and often essential role in the maintenance of wildlife communities in the adjacent upland habitats (Hirsch and Segelquist 1978). Intergradation of riparian vegetation with the adjacent upland habitat provides increased structural diversity for wildlife and creates important habitat for the survival and reproduction of many species (Thomas et al. 1979, Oakley et al. 1985). The diverse composition and structure of vegetation and the variability in soil moisture in riparian areas may influence many species of wildlife by providing food and other essential resources. Thomas et al. (1979) suggested that riparian habitat provides a source of cover, food, and water to small mammals dispersing to different habitats. Campbell and Franklin (1979) were able to identify distinct plant communities within riparian and upland areas using a gradient approach.

The distinct vegetative communities and microclimates in riparian areas, along with their rarity (e.g. less than 1% of Western United States, Knopf et al. 1988) and linear nature, makes them sensitive to habitat loss and alterations. Hirsch and Segelquist (1978) and Hair (1988) cited the urgency of preservation of remaining riparian habitat, with an estimated 70-90% of all natural riparian areas already lost in the Eastern United States. Human disturbance of natural communities including timber harvesting, livestock grazing, road building, channeling and dam building has increased (Hall 1988). Changes in stream morphology, water quality, and vegetation often result from these disturbances, followed by a decrease in the productivity of aquatic systems and the terrestrial vertebrate community (Kauffman 1988). Ultimately, these changes produce a shift in dominance to the more adaptable species, which are associated with disturbed habitats (Kauffman 1988).

The importance of maintaining riparian forest vegetation for the benefit of fish populations on larger fish bearing streams has been recognized for years (Meehan et al. 1977, Sedell et al. 1982). However the importance to other vertebrates, especially on smaller streams, is less clear. Despite the large proportion of the vertebrate community that is comprised of small mammals (approximately 38 small-mammal species, Cross 1988), the significance of riparian areas to these species is not well documented. Simons (1985) found similar small-mammal communities between old-growth and logged riparian areas in the Siskiyou

[1]Current address: 1451 N. Northview Road, Oak Harbor, WA 98277

© 1998 by the Northwest Scientific Association. All rights reserved.

Range of Northern California. Small-mammal species richness was higher in riparian areas compared with adjacent fringe or upland habitats in the Oregon Cascades (Anthony et al. 1987, Cross 1985, and Doyle 1990). In addition, Anthony et al. (1987) suggested that mammalian insectivores could be particularly sensitive to alterations in riparian habitats in parts of the Cascade mountains. According to Cross (1985), use of riparian habitat was not restricted to obligate species; some rodents with larger home ranges utilized riparian components for part of their daily and seasonal activity.

We compared species composition and relative abundance of small mammals between riparian and upland habitats and among five seral stages. We hypothesized that there were differences in small mammal communities amongst seral stages, between riparian and upland habitats, and along the inter-riparian transects. We also comment on the importance of small perennial (second-forth order) mountainous streams for riparian associated mammals and their conservation.

Methods

Study sites

Fifteen study sites were located along perennial streams in the Central Coast Ranges, Lincoln and Benton Counties, Oregon. Franklin and Dyrness (1973:31-32) described the Coast Ranges as a zone which receives 170-300 cm of precipitation a year with average temperatures that seldom drop below 0° C in winter and never exceed 27° C in summer. Organic matter content is high and acidity is medium (Franklin and Dyrness 1973:9-10).

We located three study sites for each of five seral stages (Hall et al. 1985) including: (1) shrub conifer forests; 5-10 years old, trees <3 m tall, dbh <2.5 cm, <40% crown cover, with grass-forb condition intermittent, dominant tree species Douglas-fir (*Pseudotsuga menziesii*) (2) open sapling-pole conifer forests; 20-35 years old, trees usually >3 m tall, dbh 2.5-10 cm, <60% crown cover, dominant tree species Douglas-fir (3) large sawtimber conifer forests; 110-200 years old, trees usually >30 m tall, dbh >53 cm, 60-80% crown cover, dominant tree species Douglas-fir (4) old-growth conifer forests; 200+ years old, multilayered vertical structure, 60-80% crown cover, dominant tree species Douglas-fir and western hemlock (*Tsuga heterophylla*) and (5) deciduous forests; >70% cover, dominant tree species red alder (*Alnus rubra*) and bigleaf maple (*Acer macrophyllum*). The shrub, pole and deciduous seral stages regenerated following timber harvests, and the large sawtimber and old-growth seral stages developed after wildfires. Each stand had the same seral stage on both sides of the stream and was large enough to include the transects plus a buffer of at least 100-m to reduce edge effects. Aerial photos and field reconnaissance were used to locate the sites. The elevation of the study sites ranged from 110-378-m and slope was from 28 to 68%.

We measured habitat variables in 10-m radius plots at the trapping stations from June-September, 1990. The dominant tree species along the riparian transects was red alder, the dominant deciduous shrubs were salmonberry (*Rubus spectabilis*) and stinking current (*Ribes bracteosum*); the most common evergreen shrub was salal (*Gaultheria shallon*). In contrast, the dominant tree along the upland transects was Douglas-fir, the dominant deciduous shrubs were vine maple (*Acer circinatum*) and red huckleberry (*Vaccinium parvifolium*), and the most common evergreen shrubs were salal and Oregon-grape (*Berberis nervosa*).

Trapping Design and Method

The trapping design on each study site consisted of one 350-m riparian transect, one 350-m upland transect (200-m upland and parallel to the riparian transect), and two 200-m inter-riparian transects that attached to the ends of the riparian and upland transects in a rectangular arrangement. Eight trap stations with two pitfall traps/station were located at 50-m intervals along the riparian and upland transects and nine trap stations at 25-m intervals along the inter-riparian transects. The shorter distances between stations along the inter-riparian transects were chosen to provide an accurate measure of riparian influence. Greater distances were used between the riparian and upland stations to get a larger sample area of those habitat types. There were 60 pitfall traps per stand and a total 900 traps for all stands combined. Each pitfall trap (two #10 sized cans taped together at the ends) was placed within a 10-m radius of the station center by a fallen log, stump, live tree, rock, or slope break, which acted as natural drift fences. Pitfall traps with water were used in this study and all animals were removed from the sites, frozen, and examined later for positive identification.

The study included four 28-day trapping periods during May (cool-wet season) and August (hot-dry season) of 1989 and 1990. Each trap was checked weekly resulting in 100,800 trap nights. Occasionally there were specimens that were too decomposed to identify ($\underline{n} = 22$), these animals were not included in the data set.

Statistical Analyses

All data analysis was conducted using the SAS software system (SAS Institute 1987). The null hypothesis that relative abundance of each species did not differ among seral stages was tested using one-way Analysis of Variance (ANOVA) and Student-Newman-Kuels (SNK) mean comparison tests (Devore and Peck 1986:557). The null hypothesis that relative abundance of each species did not differ between riparian and upland habitats among seral stages, and stations along the inter-riparian transects among seral stages was tested using two-way ANOVA and Student-Newman-Kuels (SNK) mean comparison tests. SNK was chosen for power in detecting significant differences and because it works well with equal sample sizes. The seral stage-by-transect interaction and seral stage-by-station interaction were used to test the transect and station effects along the inter-riparian gradient, respectively. When necessary, variables were transformed [log10 (x+1) and arc sine square-root for percent cover] to correct for non-normality or to obtain homogeneous variances. In some cases transformations were unsuccessful in producing normally distributed variables or homogeneous variables. Although seasonal comparisons were made, some seasonal variation in capture rates (total captures at each trap station over all seasons and years) might occur due to trap removal in subsequent seasons. Comparisons were made between habitats and between transects for each species individually. Results for some species were not included, because small sample sizes ($\underline{n} < 20$ captures) made statistical analyses and interpretations tenuous.

Results

A total of 9,764 individuals representing 20 species of small mammals were captured. Species richness among the seral stages was similar (15 and 16 species, excluding the non-target species)(Table 1). The total captures were progressively lower from young shrub stands to the older mature coniferous forests and highest in the deciduous stands. Species richness was similar between riparian (18 species) and upland habitats (17 species)(Table 2). There were 400 more captures along the riparian than along the upland transects.

Insectivores

The 7,793 (~80% of all captures) insectivores captured included three mole and four shrew species. *Sorex trowbridgii* and *S. pacificus* together accounted for 86% of the insectivores and 69% of all small mammals captured. *S. trowbridgii* was captured more frequently in pole and deciduous seral stages ($P < 0.01$), but it was abundant in all of the seral stages (Table 1). *Sorex vagrans* and *Scapanus townsendii* were more abundant in the shrub seral stage ($P < 0.05$) than in any of the other seral stages (Table 1). *S. bendirii* was captured about 1.8 X more often in the large sawtimber seral stage than in all other stages (Table 1). The capture rate of *Neurotrichus gibbsii* was greatest ($P < 0.05$) in the deciduous seral stage (Table 1).

The capture rate of *S. vagrans* was at least 3 X greater in the upland of the shrub habitat than in the other seral stages along the riparian and upland transects ($P < 0.05$), and the capture rate along the riparian and upland transects was different among the forest types for *N. gibbsii* ($P < 0.05$) (Figure 1). *Sorex pacificus* and *Sorex bendirii* were more abundant along the riparian than upland transects ($P < 0.001$)(Table 2). In addition, capture rates of both species along inter-riparian transects were higher near riparian areas than further away ($P < 0.001$)(Figure 2).

There was significant variation in capture rates between seasons along the riparian and upland transects for *N. gibbsii, S. pacificus*, and *S. trowbridgii* (Figure 3); however because of significant interaction between season and transect in the analysis, these results are difficult to interpret. The distribution of captures within seasons changed from 1.5 X more individuals along the riparian transect in the spring ($P < 0.01$) to 2.2 X more individuals upland in the summer for *N. gibbsii* (Figure 3). There were 1.8 X more captures of *S. pacificus* along the riparian versus upland transect ($P < 0.01$) in the spring compared to only 1.1 more captures along riparian versus upland transect in the summer. Although there was not a

TABLE 1. Average number of small-mammal captures among the five different forest seral stages (n=3) in the Oregon Coast Ranges, 1989-1990. Letters (a and b) are used to distinguish between means with significant differences.

Species	SERAL STAGE[1] S $\bar{X}$	S SE	P $\bar{X}$	P SE	L $\bar{X}$	L SE	O $\bar{X}$	O SE	D $\bar{X}$	D SE	Total Captures	P[2]
Insectivores												
Neurotrichus gibbsii	14.7	2.7b	15.3	1.3b	26.7	8.7ab	27.0	3.5ab	35.7	4.7a	358	0.0247
Scapanus orarius	1.3	0.7	5.0	2.0	5.3	1.2	7.7	2.7	8.7	4.6	84	0.3838
Scapanus townsendii	5.3	1.7a	0.3	0.3b	1.0	0.6b	0.7	0.7b	2.3	1.3ab	29	0.0382
Sorex bendirii	22.7	7.2	22.3	4.1	51.0	10.3	23.0	7.2	27.3	0.9	439	0.0556
Sorex pacificus	115.7	25.3	141.7	23.6	114.3	27.4	77.7	6.8	122.0	19.7	1714	0.3389
Sorex trowbridgii	208.0	59.5b	403.7	23.7a	290.0	17.1b	275.0	15.9b	468.3	50.5a	5016	0.0030
Sorex vagrans	33.0	6.1a	0.6	0.3c	3.0	1.5bc	3.7	2.7bc	10.7	2.0ab	153	0.0017
Subtotals	1202.0		1848.0		1474.0		1244.0		2025.0		7793	
Rodents												
Aplodontia rufra	4.7	1.7	3.0	1.7	3.7	0.9	0.3	0.3	1.7	0.9	40	0.1226
Clethrionomys californicus	21.3	15.2	18.7	2.7	45.3	16.8	56.0	20.1	4.0	3.1	436	0.0549
Microtus longicaudus	3.7	1.5	1.3	0.3	2.3	1.9	3.3	3.3	1.3	1.3	36	0.8627
Microtus oregoni	75.7	29.8a	5.7	1.5b	3.7	1.2b	2.3	0.7b	8.3	4.9b	287	0.0061
Microtus townsendii	5.3	3.2	0.7	0.7	0.3	0.3	0.0	0.0	1.0	0.6	22	0.2006
Peromyscus maniculatus	61.3	13.2a	7.3	2.7b	7.7	2.4b	5.0	1.2b	20.7	1.5b	306	0.0007
Phenacomy albipes	5.3	2.7	4.7	1.7	1.3	0.9	2.3	1.2	6.0	2.3	59	0.4827
Phenacomy longicaudus	0.7	0.3b	0.3	0.3b	1.3	0.3b	5.3	2.4a	0.0	0.0b	23	0.0033
Zapus trinotatus	47.0	26.3a	20.7	4.5b	23.0	9.3b	10.0	6.2b	33.3	10.4b	702	0.0096
Subtotals	975.0		187.0		266.0		254.0		229.0		1911	
Total Captures[3]	2191.0		2036.0		1741.0		1498.0		2257.0		9723	

[1]S=shrub, P=pole, L=large saw timber, O-old-growth, D=deciduous.

[2]One-way ANOVA with site as block and error term to test for seral stage effect. Underlined p-value indicates variable was $Log_{10} + 1$ transformed.

[3]Not including non-target species (*Mustela erminea, Thomomys mazama, Tamiasciurus douglasii,* and *Sylvilagus bachmani*) and the specimens which were in too poor condition to identify.

significant difference ($P < 0.05$) between riparian and upland captures of *S. trowbridgii* during the cool-moist season, there were 1.8 X more individuals captured in the upland during the hot-dry season ($P < 0.01$)(Figure 3).

Rodents

A total of 1,914 rodents was captured, which included 11 total species, and six of these were microtines. *Zapus trinotatus*, *Clethrionomys californicus, Peromyscus maniculatus* and *Microtus oregoni* accounted for more than 90% of the rodents captured and 18% of all small mammals captured. *P. maniculatus, M. oregoni* and *Z. trinotatus* were at least 3 X more abundant ($P < 0.01$) in the shrub stage than in the other habitats (Table 1). In contrast, *C. californicus* was captured more frequently in the large sawtimber and old-growth conifer stands and *Phenacomys longicaudus* was captured more frequently ($P < 0.01$) in the old-growth forests than in the other seral stages (Table 1). *Z. trinotatus* was captured 3.6 X more in the riparian than upland habitats ($P < 0.001$)(Table 2). It was more abundant near riparian transects than upland along inter-riparian transects ($P < 0.001$)(Figure 2). There were three microtine species that were captured 5 X more often ($P < 0.05$) in riparian than upland habitats (Table 2). *Microtus longicaudus* was captured exclusively in riparian habitat; *Microtus townsendii* also was captured almost entirely near the riparian area; and captures of *Phenacomys albipes* were significantly greater in riparian than upland habitats. In contrast, *C. californicus* was captured 6 X more

TABLE 2. Average number of small-mammal captures along stream (n=15) and upland (n=15) transects in five forest seral stages in the Oregon Coast Ranges, 1989-90.

Species[1]	Transect: Stream $\bar{X}$	Stream SE	Upland $\bar{X}$	Upland SE	Total Captures	P[2]
Insectivores						
Scapanus orarius	1.5	0.4	1.7	0.4	47	0.6495
Scapanus townsendii	0.3	0.1	0.1	0.1	6	0.4238
Sorex bendirii	24.2	3.3	1.3	0.4	383	0.0001
Sorex pacificus	40.6	3.6	26.0	3.4	997	0.0007
Sorex trowbridgii	83.7	6.7	100.3	11.9	2760	0.1884
Subtotals	2419.0		2112.0		4531	
Rodents						
Aplodontia rufra	0.9	0.3	0.5	0.2	20	0.2845
Clethrionomys californicus	2.4	1.3	14.4	3.3	253	0.0009
Microtus longicaudus	2.4	0.8	0.0	0.0	36	0.0066
Microtus oregoni	3.4	1.4	7.6	4.5	165	0.3663
Microtus townsendii	1.3	0.8	0.0	0.0	20	0.0457
Peromyscus maniculatus	5.1	1.7	6.1	1.8	167	0.2843
Phenacomys albipes	2.1	0.6	0.4	0.2	38	0.0113
Phenacomys longicaudus	0.4	0.3	0.5	0.2	13	0.7787
Zapus trinotatus	24.9	6.1	6.9	3.7	477	0.0001
Subtotals	644.0		545.0		1089	
Total Captures[3]	3066.0		2662.0		5728	

[1]*N. gibbsii* and *S. vagrans* were not included because of significant differences among forest seral stages between stream and upland transects for these species (refer to figure 1).

[2]Two-way ANOVA with transect by seral stage interaction used to test for transect effect and site by seral stage used as an error term. Underlined p-value indicates variable was Log10 +1 transformed.

[3]Not including non-target species (*Mustela erminea, Thomomys mazama, Tamiasciurus douglasii, Sylvilagus bachmani*), and the specimens which were in too poor condition to identify.

frequently ($P < 0.001$) in upland habitat (Table 2). It was the only species which was significantly more abundant at distances further from riparian transects ($P < 0.001$)(Figure 2).

Z. trinotatus was the only rodent species with significant seasonal variation in captures on the riparian and upland transects. It was captured more often in the cool-wet season than the hot-dry season ($P < 0.01$) along the riparian and upland transects (Figure 3). In addition, *Z. trinotatus* was 4.7 X more abundant along the riparian versus upland transects in the cool-wet season, but only 2.7 X more abundant along the riparian transect in the hot-dry season.

Discussion

There are a multitude of factors affecting activity and dispersion of small mammals, and animal densities alone may not always be an accurate means of measuring habitat quality of a species (Van Horne 1983). Our study does not measure the complexity of the landscape or vertebrate community; nevertheless we feel the strength in capture patterns gives validity to the results. We use these results to make important interpretations and suggest forest management implications for some species.

P. longicaudus and *C. californicus* were significantly more abundant in the old-growth and large saw timber seral stages than in the other seral stages in this study, and captures of *N. gibbsii* were progressively lower from old-growth to the younger conifer seral stages. Similarly, Carey and Johnson (1995) and Aubrey et al. (1991) found *N. gibbsii* more abundant in old-growth than in managed conifer stands. However, captures of *N. gibbsii* were even higher in the deciduous stands

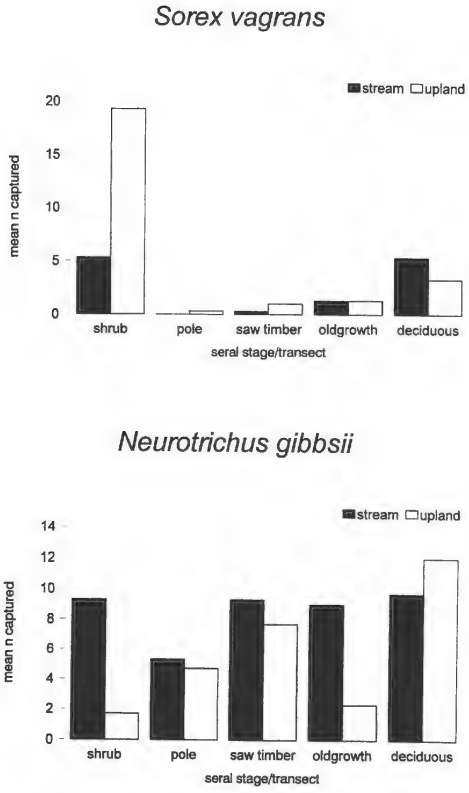


Figure 1. Mean number of *S. vagrans* and *N. gibbsii* captured among five forest types along riparian (n=3) and upland (n=3) transects in the Oregon Coast Ranges, 1989-90.

than in the mature conifer seral stages in this study, and we suggest that they might prefer the cool moist microclimates associated with mature deciduous and coniferous forests. Our results are also consistent with Corn and Bury (1986 and 1991) and Aubrey et al. (1991) for *P. longicaudus* and with Macnab and Dirks (1941), Maser et al. (1981) and Cross (1985) for *C. californicus*.

S. vagrans, S. townsendii, P. maniculatus, M. oregoni, Z. trinotatus were significantly more abundant in the shrub habitats than in other seral stages of this study. *S. vagrans* was found in a variety of habitats including lowland grasses, open brush, woods, moist meadows, headland shrub and prairie, tideland river habitats and dry uplands by others (Bailey 1936, Maser et al. 1981, Christenson and Larrison 1982). Corn and Bury (1991) found *S. vagrans* more abundant in mature (80-120 years) than young (40-75 years) and old-growth stands (150-525 years), but with the exception of the old-growth replicates, the stands they compared were of a different age and structure than those in this study. Some have suggested that *S. townsendii* occupies open habitats, mostly in wet pasture lands and agricultural fields of lowland valleys (Bailey 1936, Maser et al. 1981, Christenson and Larrison 1982). These habitat preferences might have resulted in limited numbers of captures in this study, although Maser et al. (1981) suggested that this species is sometimes found in headland prairie and shrub habitats. The fossorial habits of moles may limit the captures of this group even when drift fences are used with pitfalls (Briese and Smith 1974).

Riparian Associates

S. pacificus, S. bendirii, M. longicaudus, M. townsendii, P. albipes and Z. trinotatus were more abundant along riparian than upland transects, and they are likely to depend on small perennial streams for at least part of their life requirements on the Oregon Coast Range. *S. pacificus, S. bendirii* and *Z. trinotatus* had a strong association with riparian habitat; all were more abundant closer to the riparian areas along inter-riparian transects. The association of *S. bendirii* with riparian habitat was particularly strong: it should be considered an obligate species of riparian habitat and require riparian areas for survival on the Central Oregon Coast. The results from our study are similar to that of McComb et al. (1993), who found that *S. pacificus, S. bendirii* and *Z. trinotatus* were more abundant closer to riparian areas along inter-riparian transects, and *S. bendirii, Z. trinotatus, Microtus longicaudus and P. albipes* were more abundant along riparian than upland transects in their study. In addition, they found *P. maniculatus* and *N. gibbsii* were more abundant closer to the riparian area along inter-riparian transects. Maser et al. (1981) also suggested an association with riparian habitat for *S. pacificus, S. bendirii, M. longicaudus, M. townsendii, P. albipes* and *Z. trinotatus* on the Oregon Coast. Our results compare well with Bailey (1936), and Christenson and Larrison (1982) for *S. pacificus, S. bendirii*, and *M. townsendii*; with Ingles (1965) for *Microtus longicaudus*; and with Maser and Johnson (1967) for *P. albipes*. Doyle (1990) also found *Z. trinotatus* to be more abundant along the riparian

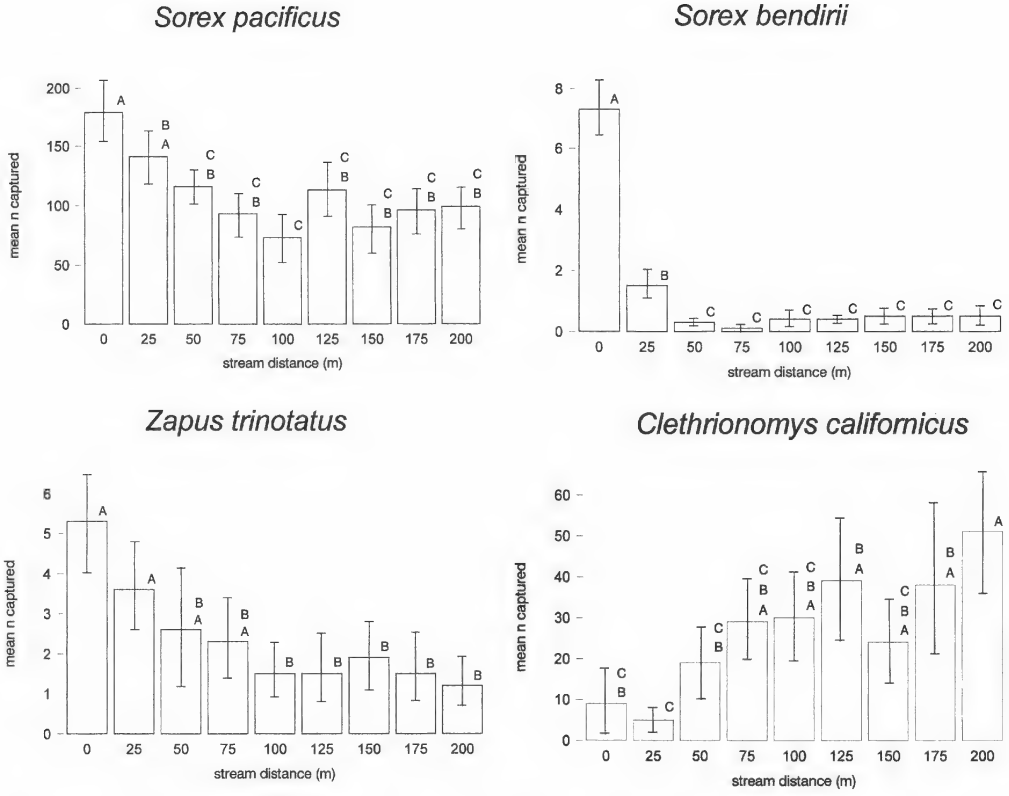


Figure 2. Mean number of *S. pacificus*, *S. bendirii*, *Z. trinotatus*, and *C. californicus* captured (±standard error) along interriparian transects (n=15) in the Oregon Coast Ranges, 1989-90. Letters (A and B) are used to distinguish between means with significant differences. Significantly different means will not share the same letter.

areas than upland and Cross (1985) found them almost entirely in the riparian areas of forests, but even more frequently in the riparian areas of clear-cuts. In addition, Ingles (1965) found them affiliated more with grassy, moist meadows located in coniferous forests. Our data suggest *Z. trinotatus* has an association with herbaceous vegetation with greater abundances in riparian areas of all the seral stages except shrub stands. In contrast, *S. bendirii* showed an affinity to all riparian areas and to the large saw timber seral stage where canopy closure was the greatest.

We conclude that small riparian systems are important habitat for small mammals and should be considered in management plans. The effect of dramatic habitat alterations on small mammal populations can be devastating particularly because many small mammal species have limited geographic ranges. Although it was ubiquitous among the seral stages in this study, *P. albipes* is one species which is naturally rare and considered sensitive in Oregon. They have been captured infrequently in a variety of habitats and have been captured most often in alder-dominated riparian areas (McComb et al. 1993 and in this study). However, this finding might be more a result of the emphasis in recent years on study and management of riparian areas, and instead *P. albipes* might be more dependent on deciduous vegetation often found in, but certainly not restricted to riparian areas. This would support Voth et al. (1983) who considered *P. albipes* to be closely associated with habitats dominated by deciduous trees and shrubs.

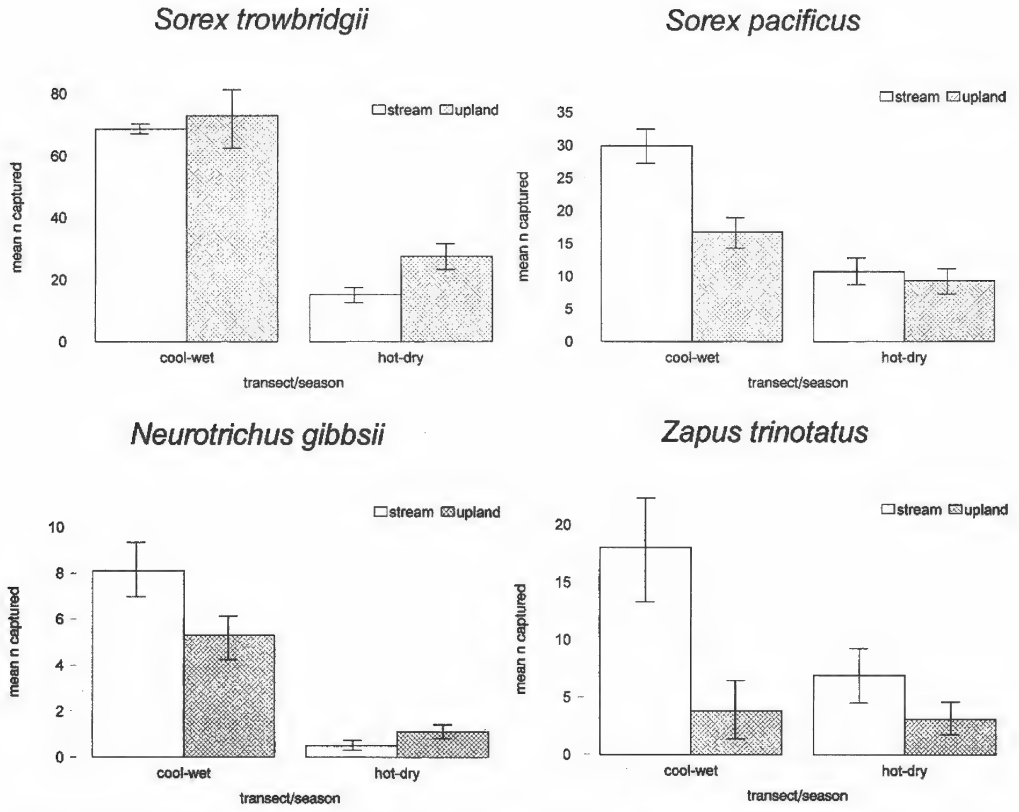


Figure 3. Mean number of *S. trowbridgii*, *S. pacificus*, *N. gibbsii*, and *Z. trinotatus* captured (±standard error) in riparian (n=15) and upland (n=15) areas during different seasons in the Oregon Coast Ranges, 1989-90.

Capture frequencies along inter-riparian transects for *S. bendirii, S. pacificus* and *Z. trinotatus* allow us to suggest zones along riparian areas for management of riparian associates. There was a significant decline in captures of these species at distances of 50-100 m from riparian transects. Consequently, riparian management zones should be at least 75-100 m on each side of perennial streams to include riparian habitat features and areas of highest abundance of all riparian associated small mammals, and to allow a buffer area which might help reduce the impact of a disturbance. These recommendations exceed current guidelines established under the Oregon Forest Practices Act, which maintain riparian management areas only on fish-bearing streams, within an average of three times the stream width, or a maximum of 30.3-m wide. Without proper forest management of riparian habitat, the status of many species' populations might be affected, functional riparian communities lost and the overall biotic potential of the riparian ecosystem limited (Kauffman 1988). Rochelle et al. (1988) suggested that specific wildlife goals for riparian areas include the maintenance or enhancement of critical riparian species, maintenance of important habitat features (down logs, snags, etc.), enhancement of cover conditions, and optimum species diversity.

P. longicaudus and *C. californicus* were significantly more abundant in the old-growth and large saw timber seral stages than in the other seral stages in this study; and *C. californicus* was significantly more abundant in the upland than in the riparian habitat (Doyle 1990) and at distances farther from riparian areas in this study and McComb et al. (1993). Management for upland/old forest associates

(*C. californicus* and *P. longicaudus*) may be equally as important as for riparian species. Management for these species should include maintenance of mature forest structural components and include upland habitat corridors. Our results are in agreement with McComb et al.; they suggest riparian buffers in mature forests of Western Oregon may not provide sufficient habitat for western red-backed voles unless they are substantially wider than necessary for riparian associates, to include linkages to upland forest patches. Whether it is management for riparian or upland associates, the approach taken should be tailored to meet the specific requirements of each species in a given area. A comprehensive approach to stream side management should include the transition and upland areas as well as the riparian zones.

The optimal size of the riparian management area for small mammals may vary geographically and temporally. Therefore, we recommend guidelines be incorporated into timber harvest plans that test the adequacy of our prescribed riparian buffer zone to meet the needs of all riparian associated small mammals within a given geographic area.

Acknowledgements

This study was conducted as part of the Coastal Oregon Productivity Enhancement (COPE) Program. Financial support for the COPE program is provided to Oregon State University College of Forestry by the USDA Forest Service, the USDI Bureau of Land Management, other federal and state agencies, forest industry, county governments, and the Oregon Small Woodland Association. We thank William McComb, Joseph Beatty, Kevin McGarigal, Melanie Bonichsen, Gody Spycher, Tom Sabin, and all those who assisted in the field.

Literature Cited

Anthony, R. G., E. D. Forsman, G. A. Green, G. Witmer, and S. K. Nelson. 1987. Small mammal populations in riparian zones of different aged coniferous forests. Murrelet 68:94-102.

Aubrey, K. B., M. J. Crites, and S. D. West. 1991. Regional patterns in small mammal abundance and community composition in Oregon and Washington. *In* L. F. Ruggiero, K. B. Aubrey, A. B. Carey, and M. H. Huff, technical coordinators. Wildlife and vegetation of unmanaged Douglas-fir forests. United States Forest Service General Technical Report PNW-285. Pp. 285-294.

Bailey, V. 1936. The mammals of life zones of Oregon. North American Fauna 55:1-416.

Briese L. A., and M. H. Smith. 1974. Seasonal abundance and movement of nine species of small mammals. Journal of Mammalogy 55:615-629.

Campbell A. G. and J. F. Franklin. 1979. Riparian vegetation in Oregon's Western Cascade Mountains: Composition, biomass, and autumn phenology. Bulletin number 14. Coniferous Forest Biome Ecosystem Analysis Studies. Seattle, Washington. 90pp.

Carey, A. B. and M. L. Johnson. 1995. Small mammals in managed, naturally young, and old-growth forests. Ecological Applications 5(2):336-352.

Christenson, J. R., and E. J. Larrison. 1982. Mammals of the Pacific Northwest. A pictorial introduction. Univ. Press of Idaho, Moscow. 166 pp.

Corn, P. S., and R. B. Bury. 1991. Small mammal communities in the Oregon Coast Range. *In* L. F. Ruggiero, K. B. Aubrey, A. B. Carey, and M. H. Huff, technical coordinators. Wildlife and vegetation of unmanaged Douglas-fir forests. United States Forest Service General Technical Report PNW-285. Pp. 241-256.

Corn, P. S., and R. B. Bury. 1986. Habitat use and terrestrial activity by red tree voles (*Arborimus longicaudus*) in Oregon. Journal of Mammalogy 67:404-406.

Cross, S. P. 1985. Responses of small mammals to forest riparian perturbations. *In* Proc. Conf. on Riparian ecosystems and their management. United States Forest Service General Technical Report RM-120. Pp. 269-275 .

Cross, R. B. 1988. Riparian Systems and Small Mammals and Bats. *In* K. Raedeke (ed.) Streamside management: riparian wildlife and forestry interactions. Symposium proceedings, Univ. of Washington, Seattle. Pp. 93-112.

Devore, J. L., and R. L. Peck. 1986. Statistics, the exploration and analysis of data. West Publishing Company. St. Paul, MN 699 pp.

Doyle, A. T. 1990. Use of riparian and upland habitats by small mammals. Journal of Mammalogy 71:14-23.

Franklin J. F., and C. T. Dyrness. 1973. Vegetation of Oregon and Washington. United States Forest Service General Technical Report PNW-80. 417pp.

Hair, J. D. 1988. Riparian habitat: Love it and leave it. *In* K. Raedeke (ed.) Streamside management: riparian wildlife and forestry interactions. Symposium proceedings, Univ. of Washington, Seattle. Pp. 1-4.

Hall, F.C., L. W. Brewer, J. F. Franklin, and R. L. Werner. 1985. Plant communities and stand conditions. *In* E. R. Brown (ed.) Management of wildlife and fish habitats in forests of Western Oregon and Washington. United States Department of Agriculture Forest Service Publication R6-F & WL-192-1985. Pp. 17-31.

Hall, F. C. 1988. Characterization of riparian systems. *In* K. Raedeke (ed.) Streamside management: riparian wildlife and forestry interactions. Symposium proceedings, Univ. of Washington, Seattle. Pp. 7-12.

Hirsch, A. and C. A. Segelquist. 1978. Protection and management of riparian ecosystems: Activities and views of the U.S. Fish and Wildlife Service. *In* R. R. Johnson and J. R. McCormick (tech. coords.) Strategies for protection and management of floodplain wetlands and other riparian ecosystems. United States Forest Service General Technical Report WO-12. Pp. 228-235.

Ingles, L. G. 1965. Mammals of the Pacific States. Stanford Univ. Press, Stanford, Calif. 506 pp.

Kauffman, J. B. 1988. The status of riparian habitats in Pacific Northwest forests. *In* K. Raedeke (ed.) Streamside management: riparian wildlife and forestry interactions. Symposium proceedings, Univ. of Washington, Seattle. Pp. 45-55.

Knopf, F. L., R. R. Johnson, T. Rich, F. B. Samson and R. C. Szaro. 1988. Conservation of riparian ecosystems in United States. Wilson Bulletin 100:272-284.

Maser, C., and M. L. Johnson. 1967. Notes on the white-footed vole (*Phenacomys albipes*). Murrelet 48:24-27.

Maser, C., B. R. Mate, J. F. Franklin, and C. T. Dyrness. 1981. Natural history of Oregon coast mammals. United States Forest Service General Technical Report PNW-133.

McComb, W. C., K. McGarigal, and R. G. Anthony. 1993. Small mammal and amphibian abundance in streamside and upslope habitats of mature Douglas-fir stands, Western Oregon. Northwest Science 67:7-15.

Macnab, J. A., and J. C. Dirks. 1941. The California red-backed mouse in the Oregon Coast Ranges. Journal of Mammalogy 22:174-180.

Meehan, W. R., F. J. Swanson, and J. R. Sedell. 1977. Influence of riparian vegetation on aquatic ecosystems with particular reference to salmonid fishes and their food supply. *In* R.R. Johnson and D. A. Jones (tech. coords.) Importance, Preservation and Management of Riparian Habitat: A Symposium. United States Forest Service General Technical Report RM-43. Pp. 137-145.

Received 4 June 1998
Accepted for publication 3 November 1998

Oakley, A. L., J. A. Collins, L. B. Everson, D. A. Heller, J. C. Howerton and R. E. Vincent. 1985. Riparian zones and freshwater wetlands. *In* E. R. Brown (tech ed.) Management of wildlife and fish habitats in forests of Western Oregon and Washington. United States Department of Agriculture Forest Service Publication R6-F & WL-192-1985. Pp. 57-80.

Rochelle J. A., K. J. Raedeke, L. L. Hicks. 1988. Introduction: Management opportunities for wildlife in riparian areas. *In* K. Raedeke (ed.) Streamside management: riparian wildlife and forestry interactions. Symposium proceedings, Univ. of Washington, Seattle. Pp. 135-138.

SAS Institute. 1987. SAS Procedures Guide For Personal Computers, Version 6 ed. Cary, NC: 373 pp.

Sedell, J. R., F. H. Everest, and E. J. Swanson. 1982. Fish habitat and streamside management: past and present. *In* Increasing Forest Productivity: Proc. Soc. Am. For. Conf., Soc. Am. For. Publ: #82-01, Washington D.C. Pp. 244-255.

Simons, L. H. 1985. Small mammal community structure in old-growth and logged riparian habitat. *In* Proc. Sympos. Riparian ecosystems and their management. United States Forest Service General Technical Report RM-120. Pp. 505-506.

Thomas, J. W., C. Maser. and J. E. Rodiek. 1979. Riparian zones. *In* Thomas, J. W. (tech. ed.) Wildlife habitats in managed forests: The Blue Mountains of Oregon and Washington, p. 40-47. United States Department of Agriculture Forest Service, Agriculture Handbook 553. Washington D.C.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47: 893-901.

Voth, E. H., C. Maser, and M. L. Johnson. 1983. Food habits of *Arborimus albipes*, the white-footed vole, in Oregon. Northwest Science, 57: 1-7.

Paul T. Flanagan, Wenatchee Field Office, USDA Forest Service, 215 Melody Lane, Wenatchee, Washington 98801-5933

Penelope Morgan, Department of Forest Resources, University of Idaho, Moscow, Idaho 83844-1133

and

Richard L. Everett, Wenatchee National Forest, USDA Forest Service, 215 Melody Lane, Wenatchee, Washington 98801-5933

Snag Recruitment in Subalpine Forests

Abstract

Information on snag locations and densities is useful for managing many species of wildlife. Using a combination of belt transects, fixed plots, and aerial photographs, we recorded snag species, locations, and causal agents of tree mortality in subalpine forests in the Entiat watershed in Washington State. The overall snag density (all standing dead trees) was 51 per hectare. Subalpine fir (*Abies lasiocarpa*) and lodgepole pine (*Pinus contorta*) were the most common species of snags. Weather-related effects created more snags than any other disturbance in the period between stand-replacing fires. The density of dominant and codominant snags did not differ by aspect or slope categories, but the density of intermediate and suppressed snags was highest on steep south-facing slopes. Snag densities were lowest in stand initiation and open stem exclusion structural stages. More study is needed to determine if fire history data combined with aerial photo interpretation offer a potential method of estimating snag densities in subalpine forests.

Introduction

Size, density, and species of snags are among the numerous factors influencing local abundance of many species of animals and birds. Snags serve as sites for roosting, nesting, denning, and foraging. Snag species important to wildlife have been identified (Parks et al. 1997) and recommendations for snag density levels have been proposed for forests in the interior Pacific Northwest (Thomas et al. 1979, Bull and Holthausen 1993, Bate 1995, Craig 1995, Evans and Martens 1995). To provide snags over time, several authors suggest designating specific green trees as snag replacements (Bull et al. 1980, Cimon 1983, Schommer et al. 1993) or developing techniques to create suitably decayed living trees (Parks et al. 1996).

How a tree dies influences its longevity as a snag and its usefulness to wildlife (Bull et al. 1997). Snag longevity is site- and species-specific (Keen 1929), and is increased by larger bole diameter and shorter height (Raphael and Morrison 1987). Wildfire is an important cause of snags. Although historically common in lower elevation forest types, wildfires are infrequent in subalpine forests. The fire return interval of forests in the Pacific Northwest is 250+ years for subalpine fir plant associations, 100 to 600 years for Pacific silver fir (*Abies amabilis*) plant associations, and 500 to 1500 years for mountain hemlock (*Tsuga mertensiana*) plant associations (Agee 1993). When killed by fire, thin-barked species such as Engelmann spruce (*Picea engelmannii*), lodgepole pine, and subalpine fir dry quickly (Bull 1983), making them resistant to insects and decay fungi (Parry et al. 1996, Hadfield and Magelssen 1997) and increasing their longevity as snags. In most forests, pathogens and insects break down far more biomass than do fires (Hagle et al. 1995) and consequently contribute more snags over the course of stand development.

Studies on size, recommended densities, and wildlife use of snags in the Northwest have focused on low and mid-elevation forests (McClelland et al. 1979, Bull 1986, Dixon 1995, Bevis 1996, Steeger and Machmer 1996, Bull et al. 1997, Saab and Dudley 1997), presumably because this is where most tree harvest occurs. However, subalpine forests are extensive, covering over 1,400,000 ha in the Cascade Mountains of Washington State. Although Thomas et al. (1979) recommended snag densities for numerous plant communities including subalpine fir, the recommendations were based only on the biology and likely occurrence of species of woodpeckers in a specific plant community, and they did not consider causes of conifer mortality and

© 1998 by the Northwest Scientific Association. All rights reserved.

the importance of snags to overall plant community dynamics. Our objective was to document snag recruitment processes by analyzing the relative sizes, densities, causal agents of mortality, and species of snags in subalpine forests. This information will provide baseline data on snag availability in high elevation forests and may provide useful insight for developing snag management strategies.

Study Area

The study site is located in subalpine forests of the Entiat Ranger District, Wenatchee National Forest, on the eastern slope of the Washington Cascade Range (Figure 1). Subalpine forests encompass 32,923 ha of the Ranger District. Glacial troughs are the dominant landform of the study area (USFS 1991). Trough walls are the upper side slopes of glacially eroded U-shaped valleys and are underlain by bedrock, often with bedrock outcrops. Trough bottoms are mantled by glacial till, avalanche debris, and colluvium. Till has a sandy loam or loamy sand texture, occasionally with volcanic ash and pumice. Deposits of till, ash, and pumice are thicker on northern and eastern aspects, and thinner on southern and western aspects. Slope ranges from 60 to 90 percent on upper trough walls and 10 to 35 percent on trough bottoms. Avalanche paths are common on glacial trough walls, especially at higher elevations (Holdorf and Donahue 1990).

Elevations in the study area range from 1280 to 2150 m above sea level, and mean annual precipitation in the study area is estimated to range from 100 to 230 cm (T. R. Lillybridge pers. comm.). Subalpine forests in the upper Entiat watershed are classified into five major plant series: whitebark pine (*P. albicaulis*), subalpine larch (*Larix lyalii*), subalpine fir, mountain hemlock, and Pacific silver fir (Lillybridge et al. 1995). The westernmost forests in the study area are in the Glacier

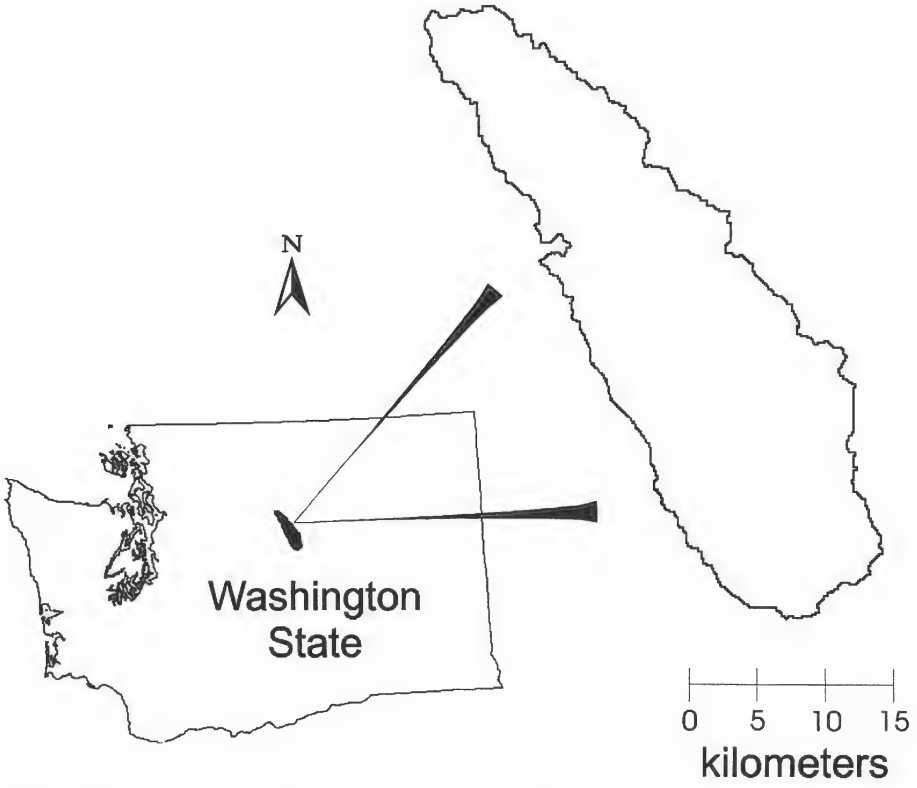


Figure 1. Location of study area in the Entiat watershed, Wenatchee National Forest.

Peak Wilderness Area. Remaining forests have a low road density and a history of little timber harvesting. Most forests within the study area have not burned for at least 100 years.

Methods

Aerial photographs taken in 1992 at a scale of 1:16,000 were used to delineate polygons, classified by predominant aspect and slope categories. Eighteen polygons were randomly selected from a total of 93. The area represented by these polygons is 5,686 ha. Stand types within polygons were subjectively classified by crown density and whether crowns had single or multiple layers. Aerial photographs were also used to assign stand types to one of seven structural stages: stand initiation, open stem exclusion, closed stem exclusion, understory reinitiation, young multi-strata, old forest multi-strata, and old forest single-stratum (Oliver 1981, O'Hara et al. 1996). Polygon and stand type boundaries were drawn on 1:24,000 scale black and white USDA Forest Service resource orthophoto quadrangles.

Both belt transects and circular fixed area plots were used to collect data. Five 9.1 m wide belt transects were established in each polygon and were oriented to cross all stand types within each polygon, beginning and ending at polygon boundaries. Belt transects were of variable lengths and compass bearings. The following data were recorded in each transect: conifer species and crown class of dead trees; starting and ending distances of stand types encountered along the transect; and whenever possible, agent(s) responsible for mortality. Crown classes were assigned according to the following criteria (Oliver and Larson 1990): dominant tree crowns that extended above the general level of crown canopy and were not physically restricted from above, and only slightly crowded by other trees on the sides; codominant trees crowns that were part of the general level of crown stratum, not physically restricted from above, and more or less crowded by other trees from the sides; intermediate trees were shorter but their crowns extended into the general level of dominant and codominant trees, were free from physical restrictions from above and quite crowded on the sides; suppressed tree crowns were entirely below the general level of dominant and codominant trees and were physically restricted from immediately above. All agents potentially contributing to mortality were recorded for each dead tree, and a determination was made of the primary agent responsible. For example, the primary agent for a tree with evidence of both moderate to aggressive root disease and bark beetle galleries was determined to be root disease. One fixed 0.02 ha plot was established where a belt transect crossed closest to the center of each stand type. Diameter at breast height (dbh) and crown position were recorded for every live and dead tree in each plot.

The Kruskal-Wallis nonparametric test was used to test two hypotheses: 1) There is no difference in snag density among six slope and aspect categories, and 2) There is no difference in snag density among structural stages. Statistical tests were performed using Statistical Analysis Systems software (SAS 1997).

Results and Discussion

A total of 6629 snags was recorded along 142 km of 9.1 m wide belt transects, representing 130 ha. The overall snag density was 51 per ha. An additional 329 snags were recorded in 77 fixed area plots. Snags were combined into two groups based on similarities in diameter: dominant and codominant snags, and intermediate and suppressed snags. Mean dbh for dominant and codominant snags was 32.5 cm (se=17.6). Mean dbh for intermediate and suppressed snags was 14.1 cm (se=10.8). The majority of the snags (83%) occupied dominant or codominant crown positions relative to the surrounding trees.

We rejected the hypothesis that there is no difference in snag density among six slope and aspect categories. The number of intermediate and suppressed snags per ha (Table 1) was significantly higher ($p < 0.05$) for steep (> 50%) south-facing slopes, which had a preponderance of relatively pure, dense lodgepole pine stands, than for other slope and aspect categories. The number

TABLE 1. Snags per hectare by aspect and slope in two crown class categories

Aspect	% Slope					
	10-30%		30-50%		50+%	
	DC†	IS	DC	IS	DC	IS
north	36	5	36	7	47	7
south	47	3	48	9	51	37•

†DC = dominant + codominant, IS = intermediate + suppressed
•significantly different from other IS values ($p<0.05$)

of dominant and codominant snags per ha (Table 1) did not differ significantly by aspect and slope categories ($p = 0.744$).

We also rejected the hypothesis that there is no difference in snag density among structural stages. Less than 1 ha in the study area was classified as old forest single-stratum. Therefore, data from old forest single-stratum and old forest multi-strata were combined. Snag density was significantly different among the six structural stages for both the dominant and codominant snag category ($p < 0.01$) and the intermediate and suppressed snag category ($p < 0.01$). A majority of the total snags (88%) were found in 4 structural stages: closed stem exclusion, understory reinitiation, young multi-strata, and old forest (Figure 2).

Although subalpine fir and lodgepole pine represented the majority of snags (Table 2), it is unknown whether or not these two species are more likely to form snags than other species because the total numbers of live stems of the different species was not recorded. The larger subalpine fir and lodgepole pine snags are suitable for some cavity nesters; a few species such as downy (*Picoides pubescens*) and three-toed (*P. tridactylus*) woodpeckers seem to prefer smaller trees (Bull et al. 1997). Both of these tree species are also important to foraging woodpeckers (Parks et al. 1997).

Weather-related effects created more snags than any other identified category (Table 2). In subalpine forests, weather may be the most consistent agent that creates snags between stand-replacement wildfires. Most of the snags killed by weather had the live crowns removed by snow, wind, or ice. Bull and Partridge (1986) report that removing the live crowns of trees with explosives or by cutting produced snags that stood a relatively long time and received the greatest nest use by woodpeckers. Top breakage allows relatively slow decay from the point of breakage downward and lowers the chance of windthrow. In contrast to trees killed by weather, trees killed by root pathogens probably stand the shortest amount of time because the decayed roots are likely to fail.

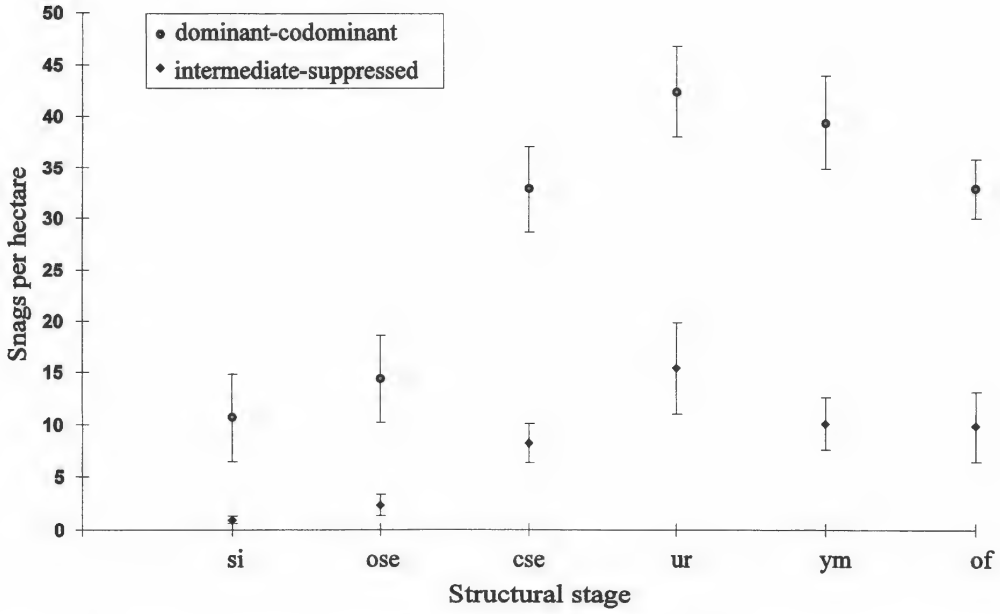


Figure 2. Snag density per hectare for two crown class categories by structural stage: si = stand initiation, ose = open stem exclusion, cse = closed stem exclusion, ur = understory reinitiation, ym = young multistrata, of = old forest. Vertical bars represent standard errors of the means.

TABLE 2. Disturbance agents affecting conifers in two crown class categories: numbers of snags per 100 hectares

Species	Weather		Animal		Root disease		Blister rust		Dwarf misteltoe		Bark beetles		Other insects		Suppressed or unknown		Total snags	
	DC[1]	IS	DC	IS	DC	IS	DC	IS	DC	IS	DC	IS	DC	IS	DC	IS	DC	IS
Engelmann spruce	52	3	6	1	88	3	-	-	-	-	102	5	5	-	74	10	327	22
Subalpine fir	378	65	15	2	176	3	-	-	-	-	17	-	45	4	628	167	1259	241
Lodgepole pine	252	25	29	1	145	28	-	-	87	3	329	31	25	-	423	269	1290	357
Douglas-fir	12	5	-	-	29	-	-	-	14	-	31	-	10	2	26	12	122	19
Whitebark pine	42	18	52	13	13	1	238	87	-	-	121	2	13	2	192	43	671	166
Subalpine larch	26	3	8	2	18	-	-	-	-	-	1	-	2	-	43	10	98	15
Pacific silver fir	19	15	2	-	52	5	-	-	-	-	15	2	12	1	86	7	186	30
Mountain hemlock	10	-	-	-	7	1	-	-	-	-	-	-	1	-	21	1	39	2
Other species	10	14	1	-	14	2	11	4	-	-	54	1	4	2	42	12	136	35
Unknown	15	-	-	-	1	1	-	-	-	-	4	-	22	-	44	3	86	4
Totals	816	148	113	19	543	44	249	97	101	3	674	41	139	11	1579	536	4214	891

[1]DC = dominant + codominant, IS = intermediate + suppressed

Bark beetles killed at least 674 trees per 100 ha, especially favoring the two pine species and Engelmann spruce (Table 2). Trees killed by bark beetles are successively colonized by a variety of insects and fungi, and provide unique habitat (Parks and Shaw 1996). Notable among the colonizers are fungi that decay sapwood, and wood boring insects.

Subalpine fir, lodgepole pine, and whitebark pine had the highest numbers of trees that died from suppression or undetermined causes (Table 2). Subalpine fir killed by insects or root pathogens deteriorates rapidly after it dies and the signs and symptoms of causal agents are soon lost. Much of the lodgepole pine mortality listed is probably attributable to suppression, because overall, 44% of the lodgepole pine snags were in the stem exclusion stage. Rodents chew the cankers on whitebark pine produced by white pine blister rust (*Cronartium ribicola*) (Mielke 1935, Hoff 1992), effectively removing evidence of infection in some cases, so it is reasonable to assume that the incidence of mortality from white pine blister rust is even higher than indicated in Table 2.

Snag creation is a combination of individual and episodic events. The size, intensity, type, and frequency of disturbances affect forest development and composition (White 1979, Gray and Franklin 1997) and also affect snag density. Disturbances such as fire or bark beetle outbreaks create pulses of snags at specific landscape locations. In this study, we recorded fewer snags in the stand initiation and open stem exclusion structural stages than might be expected. Possible reasons include reburns, which would significantly reduce snag densities in the stand initiation stage, conifer encroachment on alpine meadows, and unusual weather such as high winds or heavy wet snows that may have reduced the number of snags.

This study identified structural stages from aerial photographs and from crown class information collected in ground surveys. A logical follow-up study is to determine whether structural stages, crown classes, and vegetation types identified from aerial photographs can be combined with fire history data to provide a reasonable estimate of snag densities in subalpine forests of the Northwest.

Acknowledgements

We are grateful for assistance provided by several individuals. Tom Curd, Elizabeth Goulet, Cheryl Gross, Amy Keyes, Heidi Reisterer, Richard Schellhaas, Don Spurbeck, and Tracy Valentine collected field data; Pete Ohlson identified structural stages from aerial photographs; Roy Magelssen managed several databases and produced the figures; and Lisa Bate, Kim Mellen, and Catherine Parks provided helpful comments on the manuscript.

This project was made possible through funding by USDA Pacific Northwest Research Station, Wenatchee Forestry Sciences Lab; USDA State and Private Forestry; and the College of Fisheries, Wildlife, and Range, University of Idaho.

Literature Cited

Agee, J. K. 1993. Fire ecology of Pacific Northwest Forests. Island Press, Washington D. C. 493 p.

Bate, L. J. 1995. Monitoring woodpecker abundance and habitat in the central Oregon Cascades. University of Idaho, Moscow. M.S. Thesis. 116 p.

Bevis, K. R. 1996. Primary cavity excavators in grand fir forests of Washington's east Cascades and forestry on the Yakima Indian Nation, Washington. *In* P. Bradford, T. Manning, B. l'Anson (eds.). Proc. Wildlife tree/stand-level biodiversity. Victoria, B. C., British Columbia Environment: Pp. 77-86.

Bull, E. L. 1983. Longevity of snags and their use by woodpeckers. *In* Proc. Snag habitat management. USDA For. Serv. Gen. Tech. Rep. INT-99. Interm. For. Range Exp. Sta., Ogden, Utah. Pp. 64-67.

_____. 1986. Resource partitioning among woodpeckers in northeastern Oregon. University of Idaho, Moscow. Ph.D. Dissertation. 109 p.

Bull, E. L., and R. S. Holthausen. 1993. Habitat use and management of pileated woodpeckers in northeastern Oregon. J. Wildl. Manage. 57:335-345.

Bull, E. L., C. G. Parks, and T. R. Torgersen. 1997. Trees and logs important to wildlife in the Interior Columbia River Basin. USDA For. Serv. Gen. Tech. Rep. PNW-391. Pac. Northw. Res. Sta., Portland, Oregon. 55 p.

Bull, E. T., and A. D. Partridge. 1986. Methods of killing trees for use by cavity nesters. Wildlife Soc. Bull. 14: 142-146.

Bull, E. T., A. D. Twombly, and T. M. Quigley. 1980. Perpetuating snags in managed mixed conifer forests of the Blue Mountains, Oregon. *In* Proc. Management of western forests and grasslands for nongame birds. USDA For. Serv. Gen. Tech. Rep. INT-86. Interm. For. Range Exp. Sta., Ogden, Utah. P. 325-336.

Cimon, N. 1983. A simple model to predict snag levels in managed forests. *In* Proc. Snag habitat management. USDA For. Serv. Rocky Mtn. For. Range Exp. Sta., Fort Collins, Colorado. P. 200-204.

Craig, M. F. 1995. Pierce District cumulative effects analysis process for snag habitat. Unpubl. Rep., USFS Pierce Ranger District, Kamiah, Idaho. 5 p.

Dixon, R. D. 1995. Ecology of white-headed woodpeckers in the central Oregon Cascades. University of Idaho, Moscow. M.S. Thesis. 148 p.

Evans, D., and D. Martens. 1995. Snag and coarse woody debris guidelines for timber harvest projects. Unpubl. Rep., Payette National Forest Supervisors Office, McCall, Idaho. 24 p.

Gray, A. N., and J. F. Franklin. 1997. Effects of multiple fires on the structure of southwestern Washington Forests. Northw. Sci. 71(3):174-185.

Hadfield, J. S., and R. W. Magelssen. 1997. Wood changes in fire-killed eastern Washington tree species - Year two progress report. Unpubl. Rep., Wenatchee National Forest Supervisors Office, Wenatchee, Washington. 34 p.

Hagle, S. K., S. Kegley, and S. B. Williams. 1995. Assessing pathogen and insect succession functions in forest ecosystems. *In* L. G. Eskew (ed.). Proc. Forest health through silviculture. USDA For. Serv. Gen. Tech. Rep. RM-267. Rocky Mtn. For. Range Exp. Sta., Fort Collins, Colorado. Pp. 117-127.

Hoff, R. J. 1992. How to recognize blister rust infection on whitebark pine. USDA For. Serv. Res. Note INT-406. Interm. Res. Sta., Ogden, Utah. 7 p.

Holdorf, H. and J. Donahue. 1990. Landforms for soil surveys in the northern Rockies. Miscellaneous publication 51. Montana Forest and Conservation Experiment Station and School of Forestry, University of Montana, Missoula. 26 p.

Keen, F. 1929. How soon do yellow pine snags fall? J. For. 27:735-737.

Lillybridge, T. R., B. L. Kovalchik, C. K. Williams, and B. G. Smith. 1995. Field guide for forested plant associations of the Wenatchee National Forest. USDA For. Serv. Gen. Tech. Rep. PNW-359. Pac. Northw. Res. Sta., Portland, Oregon. 337 p.

McClelland, B. R., S. S. Frissel, W. C. Fischer, and C. H. Halvorson. 1979. Habitat management for hole-nesting birds in forests of western larch and Douglas-fir. J. For. 77:480-483.

Mielke, J. L. 1935. Rodents as a factor in reducing aerial sporulation of *Cronartium ribicola*. J. For. 33: 994-1003.

O'Hara, K. L., P. A. Latham, P. Hessburg, and B. G. Smith. 1996. A structural classification for Inland Northwest forest vegetation. West. J. Applied For. 11(3):97-102.

Oliver, C. D. 1981. Forest development in North America following major disturbances. For. Ecol. Manage. 3:153-168.

Oliver, C. D., and B. C. Larson. 1990. Forest Stand Dynamics. McGraw-Hill, Inc., New York. 467 p.

Parks, C. G., E. L. Bull, and G. M. Filip. 1996. Using artificially inoculated decay fungi to create wildlife habitat. *In* P. Bradford, T. Manning, B. l'Anson (eds.). Proc. Wildlife tree/stand-level biodiversity. Victoria, B. C. British Columbia Environment Pp. 87-89.

Parks, C. G., E. L. Bull, and T. R. Torgerson. 1997. Field guide for the identification of snags and logs in the interior Columbia River basin. USDA For. Serv. Gen. Tech. Rep. PNW-390. Pac. Northw. Res. Sta., Portland, Oregon. 40 p.

Parks, C. G., and D. C. Shaw. 1996. Death and decay: a vital part of living canopies. Northw. Sci. 70:46-53.

Parry, D. I., G. M. Filip, S. A. Willits, and C. G. Parks. 1996. Lumber and deterioration of beetle-killed Douglas-fir in the Blue Mountains of eastern Oregon. USDA For. Serv. Gen. Tech. Rep. PNW-376. Pac. Northw. Res. Sta., Portland, Oregon. 24 p.

Raphael, M., and M. Morrison. 1987. Decay and dynamics of snags in the Sierra Nevada, California. For. Sci. 33(3):774-783.

Saab, V. A., and J. Dudley. 1997. Responses by cavity-nesting birds to high-intensity wildfire and post-fire salvage logging in ponderosa pine/Douglas-fir forests of southwestern Idaho. Progress report. USDA For. Serv. Interm. Res. Sta., Ogden, Utah. 34 p.

Received 26 May 1998
Accepted for publication 4 November 1998

Schommer, T., E. Collard, and K. Widenmann. 1993. Wallowa-Whitman National Forest green tree snag replacement guidelines. Unpubl. Rep., Wallowa-Whitman National Forest Supervisors Office, Baker, Oregon. 14 p.

Statistical Analysis Systems. 1997. Release 6.12. SAS Institute Inc., Cary, North Carolina.

Steeger, C., and M. Machmer. 1996. Use of trees by cavity nesters in managed and unmanaged interior cedar-hemlock stands of southern British Columbia. *In* P. Bradford, T. Manning, B. l'Anson (eds.). Proc. Wildlife tree/stand-level biodiversity. Victoria, B.C. British Columbia Environment: Pp. 45-54.

Thomas, J. W., R. G. Anderson, C. Maser, and E. L. Bull. 1979. Snags. *In* J. W. Thomas (ed.). Wildlife habitats in managed forests. USDA For. Serv. Ag. Handb. No. 553. Washington, D. C. P. Pp. 60-77.

USFS. 1991. Wenatchee land type association map unit descriptions. Unpubl. Rep., Wenatchee National Forest Supervisors Office, Wenatchee, Washington. 9 p.

White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. Bot. Rev. 45(3):229-299.

Northwest Science Forum

Northwest Science Forum provides an opportunity to articulate and discuss scientific issues in a less structured format than peer-reviewed articles. The Forum publishes short articles, opinion pieces, and letters with a focus on science and natural resource issues in the Pacific Northwest. Although the Forum is not peer-reviewed, it is edited for format and clarity. Articles should generally be less than 2000 words and contain minimal literature citations. Letters in response to articles are particularly encouraged; the original author will normally be given a chance to respond to the letter as well. There are no page charges or reprints associated with the Forum, and participants need not be members of the Northwest Scientific Association. Please send all submissions, including two hard copies and an electronic copy (any recent version of Word or WordPerfect) to the Editor.

John F. Piatt, Alaska Biological Sciences Center, USGS, 1011 E. Tudor Rd., Anchorage, AK 99503

Marbled Murrelets *Have* Declined in Alaska

In the last issue of *Northwest Science,* Hayward and Iverson ("Long-Term Trends in Marbled Murrelets in Southeast Alaska Based on Christmas Bird Counts") failed to mention other evidence for 40-75% declines in murrelet populations, or discuss implications of a climate regime shift that has reduced populations of seabirds in Alaska, or present any useful information on the status of old-growth breeding habitat for murrelets. They examined Christmas Bird Count (CBC) data from Southeast Alaska, and concluded there is no evidence for declines in populations. They suggested that our (Piatt and Naslund 1995) previous analysis of CBC data for murrelets was erroneous, and suggested that *"the disparity between our conclusions ... invites explanation"*.

Invitation accepted. In the following, I will show that there was no disparity in conclusions, that Hayward and Iverson mis-represented our conclusions and they conducted a highly selective review of evidence for murrelet population changes in Alaska. The result was a paper that was inaccurate, incomplete, out-of-date, mis-leading and of little service to the readers of *Northwest Science* who might have read their article hoping to gain some new insight on the status of marbled murrelets in Alaska.

Piatt and Naslund (1995) reviewed information available at the time on the abundance, distribution and population status of marbled murrelets in Alaska. With regard to population trends, we stated that *"there are few quantitative data to assess population trends... We analyzed 20 years (1972-1991) of Christmas Bird Count (CBC) data in the northern Gulf of Alaska (fig. 7). Totals for each year were calculated as the sum of all murrelets seen on CBC's in Sitka, Juneau, Glacier Bay, Cordova, and Kodiak Island. We could not take the average of counts among sites (n=5) because of missing data... There was considerable inter-annual variation in total numbers, which we smoothed by taking 5-year running averages of the annual data (fig. 7). Unsmoothed data were extremely variable, and did not reveal a statistically significant trend. However, the smoothed data suggest a steady decline in abundance of about 50 percent from the early 1970's to the early 1990's."*

Thus, we clearly stated that the trend was not statistically significant and that the raw annual counts were highly variable. This is exactly the same conclusion reached by Hayward and Iverson after conducting a *"battery of statistical tests"*. Where then is the disparity? We believed that in the absence of statistical power, due largely to the extreme annual variability, that the smoothed data might still be indicating a real biological trend— a conclusion not unwarranted for the data

we considered at the time (1972-1991 only). Indeed, Hayward and Iverson themselves concluded that *"Our failure to detect a decline does not indicate that a decline has not occurred"*.

Hayward and Iverson further imply that our analysis was in several ways inadequate and at odds with their analysis. Given that we both agree the CBC trends are not statistically significant, it may be moot, but some differences deserve better explanation than those provided by Hayward and Iverson. Firstly, we analyzed data between 1972 and 1991— the latest year of data available to us at the time of our analysis. Hayward and Iverson included data in their analyses from 1992 and 1993— which contain extraordinarily high counts (see their Table 1) that would obliterate any trend; significant or otherwise. These counts, and later high counts in 1994-1996 beg explanation (see below). Secondly, Hayward and Iverson imply that their analysis is more robust because they examined data from seven sites in Southeast Alaska, while Piatt and Naslund only examined *"CBC data from a limited number of sites along the Alaska Coast"*. In fact, we deliberately chose sites with long-term data and substantial winter populations of murrelets. It is still not clear to us how analysis of data from Ketchikan (with four counts between 1972 and 1991) or Mitkof (5 counts), or Haines (11/15 zero counts from 1972-1991) would have told us anything useful about murrelets in Alaska. Thirdly, we retained missing counts in our analysis (16 out of 100 possible counts), and concluded that since most (11) of these were from the first decade (1972-1980), their absence in our analysis would tend to underestimate a downward trend, if any. Hayward and Iverson chose to fill in missing cells by taking running averages. Thus, while Hayward and Iverson imply that we evaluated trends only after we smoothed the data— the opposite is in fact true: We statistically evaluated unsmoothed, raw data while Hayward and Iverson statistically evaluated interpolated data.

The attention to details of how CBC data were analyzed by ourselves and by Hayward and Iverson distracts from the main point of concern: Have marbled murrelet populations declined in Alaska? While professing to address this point, Hayward and Iverson provide a dismal review of relevant information. From our paper, it bears repeating that compelling evidence for population change is provided by boat surveys conducted in Prince William Sound between 1972/73 and 1989/90/91: *"Based on randomly selected transects censused throughout the entire Sound, and on surveys conducted in both winter and summer, populations of* Brachyramphus *murrelets apparently declined by 67-73 percent between the early 1970's and late 1980's. Surveys in all years were conducted using similar protocols, populations estimates were relatively precise (±37-47 percent in winter, ±16-32 percent in summer), and declines observed on surveys conducted in summer were highly significant ($P<0.01$; Klosiewski and Laing 1994). Declines observed for murrelets were paralleled by population declines in 15 other marine bird species as well."*

For reasons unclear to me, Hayward and Iverson chose to focus instead on a paper by Murphy et al. (1997) which reported no change in murrelet populations in Prince William Sound (PWS) between 1984/85 versus 1989/90. Hayward and Iverson briefly mention the discrepancy between Murphy et al. (1997) and Klosiewski and Laing (1994), and imply that the difference in findings occurred simply because they *"used different methods and sampled different portions of Prince William Sound"*. How different? Murphy et al. conducted surveys in 10 bays around one island in PWS, and compared their results to a previous study (with one-time counts) that used different survey methods. As noted above, Klosiewski and Laing's (1994) surveys were statistically rigorous, covered the entire Sound, used exactly the same transects and methods employed 20 years previously on three complete replicate surveys of the entire Sound. More importantly, Murphy et al. could only examine trends over a 5-7 year period, while Klosiewski and Laing's data span nearly 20 years— notably the same period covered by the Christmas Bird Count data we analyzed (1972-1991). Why would Hayward and Iverson choose to dismiss and ignore results of the superior study?

In the same volume in which our paper appeared, Burger (1995) summarized evidence for population changes in marbled murrelets in British Columbia. Whereas CBC data provided no clear indication of trend (Rodway et al. 1992), three different boat-based studies *"are consistent in showing a significant decline in the densities of Marbled Murrelets in Clayoquot and Barkley*

sounds." Measured declines ranged between 40-75% among studies and years of comparison (Burger 1995).

Further, at the time of writing our paper, there was considerable evidence that murrelet and other seabird populations had been negatively influenced by changes in their marine environment. Hayward and Iverson state only that *"changes in the marine ecosystem in the Gulf of Alaska are purported to have reduced availability and biomass of important prey fish (Piatt and Anderson in press, as cited in Piatt and Naslund 1995)."* Apparently Hayward and Iverson have been too busy to examine the actual paper (Piatt and Anderson 1996)— preferring instead to suggest that the *"purported"* changes had no effect *"if marbled murrelet populations are not declining in response to these changes"*— a circular argument at best. In fact, ecosystem-wide changes in the Gulf of Alaska may have had a profound effect on murrelets; potentially more important than all other effects combined.

Changes in forage fish availability resulted in a dramatic change in diets of marbled murrelets from fatty species such as capelin during the 1970's to low-energy forage such as juvenile pollock during the 1980's and 1990's (Piatt and Anderson 1996, Anderson et al. 1997, Bechtol 1997, Van Pelt and Piatt 1997). Similar dramatic changes in diets of other piscivorus seabirds including murres, puffins and kittiwakes were also observed. Associated with these diet changes was a marked reduction in productivity and population size of many seabird species in the Gulf of Alaska— noted by Klosiewski and Laing in their pelagic surveys in Prince William Sound, and in studies of colonial species at their rookeries (Piatt and Anderson 1996). For example, Common murre populations declined at 15 of 16 major colonies in the Gulf of Alaska between the 1970's and 1990's, and by 40% overall (Piatt and Anderson 1996). The change in forage fish availability was associated with a marked change in ocean climate— which apparently had dramatic effects on the entire Gulf of Alaska ecosystem— including phytoplankton, zooplankton, forage fish, groundfish, salmon, marine birds and marine mammals (see reviews by Francis et al. 1998 and McGowan et al. 1998). The effects of this change in climate and food base were so pervasive, it would be extraordinary if marbled murrelets were *not* affected!

Thus, Hayward and Iverson's statements that *"a majority of the evidence leading to the inference by Piatt and Naslund (1995) that murrelets had declined by 50% in Alaska came from CBC data"* and *"It should be emphasized that we focused on CBC counts because they represent the only long-term data for this population and counts were used as the primary empirical basis for the estimate of a 50% decline in murrelets in Alaska"* are demonstrably false and misleading. The best 'empirical evidence' available suggests that marbled murrelet populations in the northern Gulf of Alaska *declined by almost 75%* and in British Columbia *by 40-75%*. A compelling body of 'empirical evidence' suggests that a climate regime shift in the Gulf of Alaska affected the entire marine ecosystem. Thus, the CBC data on murrelets should be viewed at best as a small piece of the puzzle. We were, in fact, conservative in suggesting that Alaska populations had declined by only 50%.

Hayward and Iverson also downplay concerns we and others have raised over the disappearance of marbled murrelet breeding habitat in Alaska. It is revealing of their intent when the authors state that *"Harvest of productive virgin forest in Southeast Alaska has removed 182,250 ha of old forest (or about 8% of the commercially valuable timber land) on the Tongass National Forest since 1909 (USDA Forest Service 1991); this land area does not include the significant harvest of old forest from non-federal land."* This is an extremely misleading attempt to skate around an important issue by semantics. It is now well-established that Marbled Murrelets preferentially nest in "high-volume old-growth" forest stands in Alaska (Kuletz et al. 1995a,b, Naslund et al. 1995). Further, nest-sites are usually located in the largest trees within high-volume old-growth stands (Naslund et al. 1995). Whereas all high-volume old growth may be classified as 'virgin' or 'commercially valuable', the converse is not true.

The real question is: What proportion of high-volume old-growth forest remains in Alaska? According to the Tongass Land Management Plan referred to by Hayward and Iverson, *more than 50% of high-volume old growth* in the Tongass was already gone at the time it was written. Further, as noted in Piatt and Naslund *"Substantial areas of potential nesting habitat have also been logged on state and private lands elsewhere in Alaska, principally in Prince William Sound and*

the Kodiak Archipelago... Privately-owned forests, much of which were selected or granted because of their old-growth holdings, are found in all areas of known importance to murrelets. Clearcutting is planned or underway on all privately-owned forests (Mendenhall 1992)." This is less true for Southeast Alaska, because most of the privately-owned high volume old growth has *already* been cut. A more recent threat to murrelets in southcentral Alaska has been the devastation of 3 million acres of mature forests by spruce bark beetles. In Kachemak Bay, for example, more than 90% of high-volume old-growth has been destroyed, with an apparent sharp reduction in murrelet productivity (Kuletz et al. 1997).

Finally, the most interesting issue raised by Hayward and Iverson's paper, but not addressed by them, is the marked increase in murrelet numbers on Southeast Alaska CBC counts during the 1992-1996 period. At least two hypotheses can be advanced to explain these observations. First, it may represent an actual increase in murrelet populations. However, given their low productivity (Beissinger 1995), and data discussed above, it seems unlikely that this rapid increase could be accounted for by population growth alone. Secondly, it may represent a re-distribution of winter populations. Although post-breeding dispersal patterns are poorly known (Piatt and Naslund 1995), it appears that most of the northern Gulf populations disperse southward during winter. Water temperatures in the Gulf of Alaska during the winters of 1990-1997 have all been anomalously warm (Institute of Marine Science, Univ. of Alaska, Fairbanks), perhaps because of persistent El Niño-like conditions in the North Pacific (Trenberth and Hoar 1995). Larger numbers of murrelets may be overwintering in northern waters in recent years, leading to unusually high counts on CBC's. Unusually large nearshore aggregations of common murres have also been noted during recent warm winters (Piatt and Van Pelt 1997, J.F. Piatt, Unpubl. data).

In conclusion, we are inclined to agree with Hayward and Iverson (and Burger 1995) that CBC data may not lend itself to statistical evaluation of population trends in marbled murrelets. However, a wealth of other empirical data suggests that marbled murrelets *have* declined substantially throughout their range, and populations in Alaska *are* threatened by a host of factors including loss of old-growth breeding habitat by logging and spruce bark beetles, oil pollution, gill-netting, and changes in food supply.

Literature Cited

Anderson, P.J., J.E. Blackburn, and B.A. Johnson. 1997. Declines of Forage Species in the Gulf of Alaska, 1972-95, as Indicator of Regime Shift. *In* Baxter, B. S. (Ed.) 1997. Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems November 13-16, 1996, Anchorage, Alaska. University of Alaska, Alaska Sea Grant Rep., 97-01. Pp. 531-543.

Bechtol, W.R. 1997. Changes in forage fish populations in Kachemak Bay, Alaska, 1976-1995. *In* Baxter, B.S. (Ed.) 1997. Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems November 13-16, 1996, Anchorage, Alaska. University of Alaska Sea Grant Rep., 97-01. Pp. 441-455.

Beissinger, S.R. 1995. Population trends of the Marbled Murrelet projected from demographic analyses. *In* Ralph, C.J., G. Hunt, M. Raphael, and J.F. Piatt (Eds.). Ecology and Conservation of the Marbled Murrelet. General Technical Report PSW-GTR-152. Albany, CA: Pacific Southwest Research Station, Forest Service, US Department of Agriculture. 420 pp. Pp. 385-393.

Burger, A.E. 1995. Marine distribution, abundance, and habitats of Marbled Murrelets in British Columbia. *In* Ralph, C.J., G. Hunt, M. Raphael, and J.F. Piatt (Eds.). Ecology and Conservation of the Marbled Murrelet. General Technical Report PSW-GTR-152. Albany, CA: Pacific Southwest Research Station, Forest Service, US Department of Agriculture. Pp. 295-312.

Francis, R.C., S.R. Hare, A.B. Hollowed, and W.S. Wooster. 1998. Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. Fish. Oceanogr. 7:1-21.

Klosiewski, S.P. and K.K. Laing. 1994. Marine bird populations of Prince William Sound, Alaska, before and after the *Exxon Valdez* oil spill. *Exxon Valdez* Oil Spill State and Federal Natural Resources Damage Assessment Final Report (available from the Oil Spill Public Information Office, 645 G. St., Anchorage AK 99501).

Kuletz, K.J., E. Holsten, J.F. Piatt and K. Oakley. 1997. Spruce Beetle: A serious threat to Marbled Murrelets in Alaska? Pac. Seabirds 24:28.

Kuletz, K.J., D.K. Marks, N.L. Naslund, and M.B. Cody. 1995a. Marbled Murrelet activity relative to forest characteristics in the Naked Island area, Prince William Sound, Alaska. NW Nat. 76:4-11.

Kuletz, K.J., D.K. Marks, N.L. Naslund, N.J. Goodson, and M.B. Cody. 1995b. Inland habitat suitability for the Marbled Murrelet in South central Alaska. *In* Ralph, C.J., G. Hunt, M. Raphael, and J.F. Piatt (Eds.). Ecology and Conservation of the Marbled Murrelet. General Technical Report PSW-GTR-152. Albany, CA: Pacific Southwest Research Station, Forest Service, US Department of Agriculture. Pp. 141-150.

McGowan, J.A., D.R. Cayan, and L.M. Dorman. 1998. Climate-ocean variability and ecosystem response in the Northeast Pacific. Science 281:210-217.

Murphy, S.M., R.H. Day, J.A. Wiens, and K.R. Parker. 1997. Effects of the *Exxon Valdez* oil spill on birds: Comparisons of pre- and post-spill surveys in Prince William Sound, Alaska. Condor 99:299-313.

Naslund, N.L., K.J. Kuletz, M.B. Cody, and D.K. Marks. 1995. Tree and habitat characteristics and reproductive success at Marbled Murrelet tree nests in Alaska. NW Nat. 76:12-25.

Piatt, J.F. and N.L. Naslund. 1995. Abundance, distribution and population status of Marbled Murrelets in Alaska. *In* Ralph, C.J., G. Hunt, M. Raphael, and J.F. Piatt (Eds.). Ecology and Conservation of the Marbled Murrelet. General Technical Report PSW-GTR-152. Albany, CA: Pacific Southwest Research Station, Forest Service, US Department of Agriculture. Pp. 285-294.

Piatt, J.F., and P. J. Anderson. 1996. Response of Common Murres to the *Exxon Valdez* oil spill and long-term changes in the Gulf of Alaska marine ecosystem. *In Exxon Valdez* Oil Spill Symposium Proceedings. Rice, S. D., R. B. Spies, D. A. Wolfe and B. A. Wright (Eds.). American Fisheries Society Symposium 18, Bethesda, Maryland. NMFS-AFSC-69. Pp. 720-737.

Piatt, J.F., and T.I. van Pelt. 1997. Mass-mortality of guillemots (*Uria aalge*) in the Gulf of Alaska in 1993. Mar. Poll. Bull. 34:656-662.

Rodway, M.S., H.R. Carter, S.G. Sealy, and R.W. Campbell. 1992. Status of the Marbled Murrelet in British Columbia. Pp. 17-41 *in* Carter, H.C., and M.L. Morrison (Eds.), Status and Conservation of the Marbled Murrelet in North America. Proc. West. Found. Vert. Zool. 5(1).

Trenberth, K.E. and T.J. Hoar. 1995. The 1990-1995 El Niño-Southern Oscillation event: Longest on record. Geophys. Res. Lett. 23:57-60.

Van Pelt, T., J.F. Piatt, B.K. Lance, and D.D. Roby. 1997. Proximate composition and energy density of some North Pacific forage fishes. Comp. Biochem. Physiol. 118(A): 1393-1398.

Gregory D. Hayward, Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming 82071
and
George C. Iverson, Alaska Region, U.S.D.A. Forest Service, P. O. Box 21628, Juneau, Alaska 99802-1628

The Challenge of Evaluating Population Trend for Conservation Management: Marbled Murrelets in Alaska

In 1995, while working on issues regarding management of forest lands in Southeast Alaska, we were alarmed to read that marbled murrelets (*Brachyramphus marmoratus*) throughout Alaska may have experienced a steady 50% decline in abundance of over the previous two decades (Piatt and Naslund 1995). We were alarmed because a 50% decline in a seabird population is a dramatic change; a condition demanding attention. In a conservation context, management initiated in response to this information could result in consequences for the murrelet and other species. Therefore, we asked whether Christmas Bird Count (CBC) data, the main quantitative trend information available for Alaska, suggested a similar decline for one of the states' three main areas of murrelet concentration, Southeast Alaska.

In Hayward and Iverson (1998) we examined CBC for evidence regarding the status of marbled murrelets in Southeast Alaska. The clear goal of our paper was to: examine CBC data for evidence of trend in murrelet populations in Southeast Alaska. We emphasized the limitations of CBC data to examine trend and stressed that CBC represents only one type of evidence to evaluate population status. Unfortunately, CBC data were the only long-term quantitative data on trend for murrelets in this sub-region. Ultimately, when evaluating the results of our analysis, we emphasized that "our failure to detect a decline does not indicate that a decline has not occurred, only that CBC data do not support such a conclusion." (Hayward and Iverson 1998:170).

Piatt has responded to our manuscript with a strong rebuttal (Piatt 1998). In May, 1995, we twice sent copies of our draft to Piatt with a request for dialogue. It is sad that it took over 3 years and publication of our manuscript for him to accept our invitations. Here we respond to Piatt's (1998) comments.

As many of the points raised by Piatt (1998) are clearly addressed in our original manuscript, we do not respond to them point by point. Instead, we begin by re-emphasizing the goal of our paper which Piatt (1998) mis-states. Then, we use two examples to highlight inconsistencies and errors in Piatt's rejoinder. We address questions regarding quantitative evidence for a decline and the accusation that we mislead readers regarding the potential impact of declining old-growth forest in the region. Finally, we address the point Piatt raises at the end of his rejoinder — hypotheses to explain the pattern of counts at the end of the timeline illustrated in Hayward and Iverson (1998:Table 1).

Goal of Hayward and Iverson (1998)

Throughout his rebuttal Piatt (1998) implies that we sought to evaluate the status of marbled murrelets in Alaska, suggesting at one point that "Hayward and Iverson provide a dismal review of relevant information." To the contrary, we repeatedly expressed our limited goal — to examine the only long-term data on murrelet population trend in Southeast Alaska. After presenting the results of our analysis, we placed the conclusions in perspective by comparing our analyses with the few other quantitative data from Alaska. We agreed with Piatt and Naslund (1995) that information on food resources, nesting habitat, and threats from gill netting and oil pollution all provided evidence that murrelet populations may be declining (see Hayward and Iverson 1998:170). We also emphasized the vulnerability of this species due to its life history. However, we questioned the conclusions reached by Piatt and Naslund (1995:293-294) regarding quantitative evidence for population decline based on their description of data analyses and inconsistencies between the evidence presented and inferences made.

Quantitative Evidence of Murrelet Trend

A major theme of Piatt's response is that "Marbled Murrelets Have Declined in Alaska" (Piatt 1998:TITLE PAGE) and that we overlooked the compelling evidence for the downward trend. Murrelets may have declined (Hayward and Iverson 1998), but is there sound quantitative evidence to support this population trend? In his rejoinder, Piatt supports the argument for a population decline with 2 quantitative analyses of trend from Alaska: 1) data from CBC presented in Piatt and Naslund (1995) and, 2) data from surveys in Prince William Sound first presented in Klosiewski and Laing (1994). The other quantitative assessment of population abundance presented by Piatt comes from surveys along the southern coast of British Columbia. Below we address several points Piatt makes regarding the evidence from Alaska. We do not address the studies from southern British Columbia because Burger (1995:306) notes potential difficulties interpreting these results and Wiens and Parker (1995) have thoroughly discussed the problems evaluating trend when only a single historical count is available. British Columbia surveys also represent counts geographically associated with northern Washington, where murrelets are formally recognized as threatened under the Endangered Species Act, rather than Southeast Alaska where they are not listed.

Referring to his analysis of CBC data (Piatt and Naslund 1995), Piatt (1998) defends his earlier conclusion that the visual pattern provides evidence of a steady decline in murrelet abundance. He indicates that "the smoothed data might still be indicating a real biological trend — a conclusion not unwarranted for the data we considered at the time (1972-1991 only)."(Piatt 1998:4th paragraph). Unfortunately, this conclusion *is unwarranted* for several substantial reasons. Piatt and Naslund (1995) based their conclusion on patterns observed in smoothed data AFTER performing a nonsignificant regression on the raw data (and not presenting the raw data for review). As suggested by J. Baldwin (Research Statistician, U. S. Forest Service, Pacific Southwest Station, pers. comm.) this approach has important consequences:

1) Smoothing does not add any new information to a linear regression or allow a regression more capacity to see through the variability in the data. Rather, smoothing introduces correlations among observations (violating a key assumption of regression), *and trends can frequently appear where none truly exist.* Simulation results suggest that Type I error rates increase from a predefined 5% to over 40%, due to smoothing, when applied to the CBC counts examined by Piatt and Naslund (1995). Therefore, even a visual trend may be an artifact of smoothing.

2) Any assessment of trend in smoothed data must account for the introduced error structure in the smoothed data (Barker and Sauer 1992). In this case, smoothing increases the variance of the standard slope estimate.

3) Suggesting a "steady decline" is inappropriate when no statistical test is performed on the smoothed data, considering the lack of significance with the raw data. The conclusion that a trend exists, implies that a true relationship exists between abundance and time (the nonsignificant relationship explored in regression).

4) And perhaps most important, when the reader looks at the potentially introduced trends (as in Figure 7, Piatt and Naslund 1995), the reader does not have the information to account for the correlation structure in the data.

In summary, smoothing can introduce 'false trends' at a high rate and neither Piatt and Naslund (1995) nor Piatt (1998) addressed this critical concern. To the contrary, they imply that the smoothed data presents the best representation of reality.

The second quantitative evidence Piatt (1998) uses to conclude that murrelets have declined comes from boat surveys conducted in Prince William Sound before and after the *Exxon Valdez* oil spill (Klosiewski and Laing 1994). This study found a marked decline in murrelet counts after the oil spill compared with a count 20 years earlier. Conclusions by Klosiewski and Laing (1994) differed from those of Murphy et al. (1997) regarding temporal patterns of murrelet abundance and we contrasted the two investigations in our paper (Hayward and Iverson 1998:177).

Unfortunately, Klosiewski and Laing (1994) is not a refereed paper available in the primary literature. Furthermore, biologists familiar with the surveys (pre- and post-spill) used in the Klosiewski and Laing (1994) analysis, question the comparability of survey methods (R. H. Day and S. M. Murphy, ABR Inc., Fairbanks, AK, pers.

comm.). Piatt's analysis also fails to account for the potential influence of observer bias, an important consideration in any assessment of trend (Thompson et al. 1998). Our paper did not state that either Murphy at al. (1997) or Klosiewski and Laing (1994) provided more compelling evidence regarding murrelet trend. In evaluating evidence for trend in murrelet populations in Alaska, however, the contrasting conclusions of these two papers must be considered. Piatt (1998) chooses to ignore the peer reviewed publication (Murphy at al. 1997) in evaluating the strength of evidence for trend, while we do not. In summary, the second piece of quantitative evidence is not as compelling as Piatt (1998) contends.

Murrelet Relationship with Old-growth Forest

Piatt (1998) openly questioned our treatment of information on the status of old-growth forests in Southeast Alaska. In Hayward and Iverson (1998) we emphasize that several resources important to marbled murrelets are currently experiencing negative trends. We noted the decline in high volume old forest in our introduction and declines in all classes of old-growth in our discussion. Contrary to our intent, Piatt (1998) suggests we "downplay concerns...over the disappearance of marbled murrelet breeding habitat". In doing so, however, Piatt (1998) seriously misrepresents current scientific evidence regarding relationships between murrelets and forest habitats.

Piatt (1998) indicates that "It is now well-established that marbled murrelets preferentially nest in "high-volume old-growth" forest stands in Alaska (Kuletz et al. 1995a, b, Naslund et al. 1995)." Piatt (1998) misrepresents this information in two important ways. First, the cited studies of nesting habitat relationships did not address 'preference'. Habitat preference implies choice of one habitat over others and cannot be established in descriptive studies of use (Peek 1986:82-83). The studies cited by Piatt (1998) generally documented habitat use (Naslund et al 1995) or for some variables, they compared levels of use (Kuletz 1995a). More important, however, Kuletz et al. (1995a:9) emphasized that evidence for nesting behaviors was greatest, *not in high volume old forest* as suggested by Piatt (1998), but in "moderate volume classes". Also, of the 33 murrelet nests that have been located in Alaska, only 19 (57%) were in old growth trees with the remainder being located on the ground; as were 2 of the 6 nests located in Southeast Alaska (DeGange 1996). We suggest that murrelet nesting habitat relationships are NOT "well established" for Alaska and deserve further investigation, particularly to determine whether nesting habitat is indeed a limiting factor to murrelet populations.

High CBC Counts During 1992-1996

Piatt's (1998) final argument regards our failure to explain the high murrelet numbers in CBC recorded in Southeast Alaska from 1992-1996. We see little reason to focus on the last quarter of the time series to explain the long-term temporal pattern. First, we question whether a "marked increase in murrelet numbers" is consistent across the 7 CBC sites in Southeast Alaska. An exploratory analysis of the 26 year time-series (regression and examination of mean counts) failed to demonstrate a consistent, marked-increase in numbers across sites. More important, however, we suggest that any attempt to explain pattern in the counts should address the entire time series. Focusing on the last 5 years suggests that 'explaining' the recent counts is the objective rather than understanding the factors influencing CBC overall. When Piatt and Naslund (1995) used CBC as evidence for a decline, they implied that CBC data reflect murrelet abundance. Interestingly, alternative explanations for the pattern in CBC were not offered in the initial conclusion of a 50% decline but Piatt (1998) explores alternatives when considering increasing counts.

Our decision to not focus on the high counts during the past 5 years was consistent with our objectives. We were concerned with detecting any actual decrease in abundance which is why we used one-tailed tests to increase statistical power to detect declines. Had we focused our attention toward potential increases in abundance, we might have noted that recent estimates of murrelet abundance throughout Alaska (Agler et al. 1998) more than double the estimates reported in Piatt and Naslund (1995).

Broader Message for Conservation Management

Although Piatt (1998) suggests that Hayward and Iverson (1998) did little service for readers of

Northwest Science, we stand by the conclusions reached in our paper. Efficient conservation management demands close scrutiny of population trends. Some threshold of evidence is necessary to prompt management action. It is regretful that some biologists are not interested in throwing multiple bricks of data at management hypotheses as suggested by Murphy and Noon (1991). Repeated testing of hypotheses and failure to reject them strengthens conclusions and increases scientific credibility.

Our results do not unequivocally establish that marbled murrelets in Southeast Alaska have not declined, but CBC data from the region do not provide evidence to support Piatt's (1998) conclusion that murrelets have declined substantially throughout their range in Alaska. We repeat our agreement with Piatt and Naslund (1995) that resource conditions, particularly the loss of old-growth forest nesting habitat, and changes in food resources, can pose a significant threat to murrelet populations.

Clearly we perceive murrelet trends differently than Piatt. Where he sees unequivocal evidence of a substantial decline, we suggest, as did DeGange (1996), that the data are weak and the jury is still out. Our differing conclusions have implications for management of marbled murrelets AND other sensitive species. Establishing conservation priorities depends upon evaluation of evidence regarding the status of species or ecological systems. Early identification of conservation problems has been recognized as an important step to improve management effectiveness and efficiency (Tear 1993); failure to detect a decline and to discern the cause is a critical conservation error. However, allocation of limited resources toward a perceived higher priority species, precludes use of those resources elsewhere. Therefore critical evaluation of evidence regarding conservation status is necessary to avoid serious errors in conservation planning; errors conservation biologists should seek to avoid.

The tradeoffs and shadow costs of conservation decisions have been recognized by others (e.g. Brown and Shogren 1998). Furthermore, Caughley and Sinclair (1994) emphasize the importance of identifying population trend and the specific deterministic factors influencing population declines as part of an effective conservation plan. Sorting among possible limiting factors is especially important for murrelet conservation because murrelets interact with both the marine and terrestrial system. We suggest that an enriched discussion of the species' status and relationship with resources may improve conservation efforts. For instance, if the decline in murrelet numbers illustrated in the smoothed data examined by Piatt and Naslund (1995:294) is real, then it may suggest a very different set of causal factors than the "steady decline" they describe (Piatt and Naslund 1995:293). The step decrease illustrated in Figure 7 would point toward a catastrophic change in resources (such as food resources) rather than the more gradual decline expected from change in other habitat conditions. Effective management of marbled murrelets depends on our ability to examine alternative hypotheses (Chamberlain 1965) regarding population trend and to discover the cause of documented population declines.

Acknowledgements

We thank J. Baldwin, A. Hale, D. Keinath, M. Koopman, C. Martinez del Rio, C. Nations, F. Rahel, R. Russell, C. Shaw, and H. Struempf for discussions that helped us focus on the issues and maintain perspective while writing this response.

Literature Cited

Agler, B. A., S. J. Kendall, and D. B. Irons. 1998. Abundance and distribution of marbled and Kittlitz's murrelets in Southcentral and Southeast Alaska. Condor 100:254-265.

Barker. R. J. and J. R. Sauer. 1992. Modeling population change from time series data. *In* D. R. McCullough and R. H. Barrett. eds. Wildlife 2001: populations. Elsevier Sci. Publ. London, U. K. Pp. 182-194.

Brown, G. and J. Shogren. 1998. Economics of the Endangered Species Act. Journal of Economic Perspectives 12:3-20.

Burger, A. E. 1995. Marine distribution, abundance, and habitats of marbled murrelets in British Columbia. *In* C. J. Ralph, G. L. Hunt, M. G. Raphael, and J. F. Piatt. eds. Ecology and conservation of the Marbled Murrelet. Gen. Tech. Rep. PSW-GTR-152. Pp. 295-312. Pacific Southwest Research Station, USDA Forest Service. 420 pp.

Caughley, G. and A. R. E. Sinclair. 1994. Wildlife ecology and management. Blackwell Science, Cambridge, MA. 334 pp.

Chamberlain, T. C. 1965. The method of multiple working hypotheses. Science 148:754-759.

DeGange, A. R. 1996. A conservation assessment for the marbled murrelet in Southeast Alaska. Gen. Tech. Rep. PNW-GTR-388. Pacific Northwest Research Station, USDA Forest Service. 420 pp.

Hayward, G. D. and G. C. Iverson. 1998. Long-term trend in marbled murrelets in Southeast Alaska based on Christmas Bird Counts. Northwest Science 72:170-179.

Kuletz, K. J., D. K. Marks, N. L. Naslund, and M. B. Cody. 1995a. Marbled murrelet activity relative to forest characteristics in the Naked Island area, Prince William Sound, Alaska. Northwestern Naturalist 76:4-11.

Kuletz, K. J., D. K. Marks, N. L. Naslund, N. J. Goodson, and M. B. Cody. 1995b. Inland habitat suitability for the marbled murrelet in Southcentral Alaska. *In* C. J. Ralph, G. L. Hunt, M. G. Raphael, and J. F. Piatt, eds. Ecology and conservation of the Marbled Murrelet. Gen. Tech. Rep. PSW-GTR-152. Pacific Southwest Research Station, USDA Forest Service. Pp. 141-150.

Klosiewski, S. P. and K. K. Laing. 1994. Marine bird populations of Prince William Sound, Alaska, before and after the *Exxon Valdez* oil spill. *Exxon Valdez* Oil Spill State and Federal Natural Resources Damage Assessment Final Report (available from the Oil Spill Public Information Office, 645 G. St., Anchorage AK 99501).

Murphy, D. D. and B. R. Noon. 1991. Coping with uncertainty in wildlife biology. Journal of Wildlife Management 55:773-782.

Murphy, S. M., R. H. Day, J. A. Wiens, and K. R. Parker. 1997. Effects of the *Exxon Valdez* oil spill on birds: Comparisons of pre- and post-spill surveys in Prince William Sound, Alaska. Condor 99:299-313.

Naslund, N. L., K. J. Kuletz, M. B. Cody, and D. K. Marks. 1995. Tree and habitat characteristics and reproductive success at marbled murrelet tree nests in Alaska. Northwestern Naturalist 76:12-25.

Peek, J. M. 1986. A review of wildlife management. Prentice-Hall, Englewood Cliffs, N J. 486 pp.

Piatt, J. F. 1998. Marbled Murrelets *Have* Declined in Alaska. Northwest Science 72:310-314.

Piatt, J. F. and N. L. Naslund. 1995. Abundance, distribution, and population status of Marbled Murrelets in Alaska. *In* C. J. Ralph, G. L. Hunt, M. G. Raphael, and J. F. Piatt. eds. Ecology and conservation of the Marbled Murrelet. Gen. Tech. Rep. PSW-GTR-152. Pacific Southwest Research Station, USDA Forest Service. Pp. 285-294.

Tear, T. H., J. M. Scott, P. H. Hayward, and B. Griffith. 1993. Status and prospects for success of the endangered species act: A look at recovery plans. Science 262:976-977.

Thompson, W. L., G. C. White, and C. Gowan. 1998. Monitoring vertebrate populations. Academic Press, San Diego, CA. 365 pp.

Wiens, J. A. and K, R. Parker. 1995. Analyzing the effects of accidental environmental impacts: approaches and assumptions. Ecological Applications 5:1069-1083.

Book Review

Not Just Trees: The Legacy of a Douglas-fir Forest

Jane Claire Dirks-Edmunds, 1999, Washington State University Press, Pullman, Washington ($35.00 cloth, $22.95 paper)

The growth of an ecologist and the growth, death, rebirth, structure and death again of a forest are the ingredients of this book. *Not Just Trees* blends both a personal story and a natural history of Northwest coniferous forests through a fascinating account of a patch of forest on Saddleback Mountain in the northern coast range of Oregon. In Part I, the author, originally from the plains of Kansas, recounts her introduction to coastal forests during her undergraduate years in the 1930s at Linfield College, McMinnville, Oregon. She became involved in a project initiated by Linfield faculty member James A. Macnab (nicknamed "Prof") to study the structure and workings of a coniferous forest in the coast range of Oregon. In this section, her interest and excitement in being involved in this extensive project were obvious. She and other team members spent countless hours in the field accumulating environmental data and collecting and cataloguing as much biota from their patch of forest as possible. She recounts experiences with other students who were also involved in the project over the years, and the lasting friendships that were formed. Since I am also at a four-year school, and have had the good fortune of working with several very good undergraduates over the last several years on a continuing project, I felt a close kinship with her described project and people involved.

The influence of Dirks-Edmunds' undergraduate experience with "Prof" resulted in her earning a doctorate from the University of Illinois under the famous ecologist V. E. Shelford. She used much of her data from Oregon, combined with similar studies of a patch of eastern deciduous forest, to form her dissertation.

In the early 1940s, after obtaining her Ph.D., Dirks-Edmunds returned to Oregon, eventually working into a full teaching position at Linfield College—after "Prof," who had also recently earned his doctorate, had moved on to Portland State. At this time she rekindled her studies of the forest on Saddleback. However, by then the forest had been logged, so the study became a comparison of a young developing forest with the historical mature forest it had been. Her studies at the site continued intermittently until her retirement. Macnab's studies and Dirks-Edmunds' later studies made extensive use of other systematists/ecologists throughout the country for identifications and discussions. The whole account gives a realistic view of the effort, frustration and elation accompanying research in general and field research in particular. It encouraged me to continue my studies and to involve undergraduate students in the process as much as possible.

In the second part of the book, the author uses two approaches to describe the two types of forest. First she describes the structure by groups of organisms, focusing largely on the animal component of forests. Although she writes extensively about insects, she does not neglect other invertebrates or vertebrates. Secondly, she goes into the role of the different organisms in the forest, as far as could be ascertained. Again, she deals extensively with the invertebrates and their role in recycling within the forest. Along this line, she provides a nice description of the breakdown and decay of downed trees until they become part of the forest floor. She finishes the descriptive portion with a chapter describing Macnab's interpretation of the "aspection"—seasonal flow of change in a forest. Through this part of the book, I gained a deeper appreciation of the organisms and the complexity of interactions in a forest community.

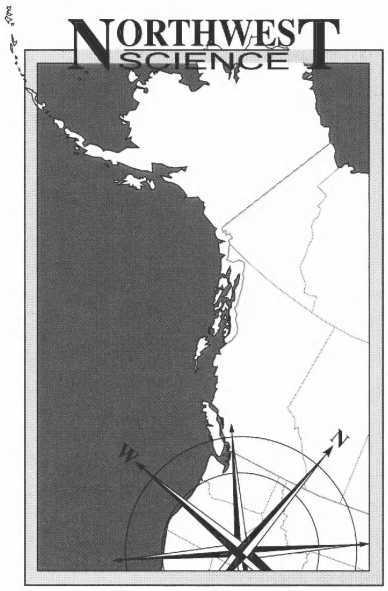
In the final segment of the book the author recounts a post-retirement visit to Saddleback Mountain, only to discover the loss of the younger forest to clear-cutting. The reader is impressed that this was a severe blow to Dirks-Edmunds, due to her love of the forest, fostered over half a century. She further comments on the general loss of old-growth forests in the Northwest and their replacement with tree farms. This account was written to preserve those lost forests in her mind, and in the minds of her readers. I think she has achieved that very successfully.

© 1998 by the Northwest Scientific Association. All rights reserved.

Not Just Trees will appeal to many different people, from those with a layman's interest in forests to professionals who work with forests. I would suggest this book as a must read for a couple of groups: 1) undergraduates in science—particularly in field-related biology, and 2) women considering careers in science. While the author does not spend much time on gender in science, she does occasionally mention the difficulties and the paucity of women in graduate programs, especially during her own era. While we have made strides to overcome them, I feel there are still obstacles that make science careers more difficult for women. The author's experience provides a strong impetus to pursue what you desire and make it fun at the same time.

—David H. Hansen, Professor
Department of Biology
Pacific Lutheran University

Join
The Northwest Scientific Association



A membership in the Northwest Scientific Association carries several benefits including subscription to the quarterly professional journal, *Northwest Science.*

Northwest Science is a refereed journal that has published original research in the basic, applied, and social sciences for over seventy years. Distributed throughout the Pacific Northwest, the United States, Canada, and more than fifty countries, *Northwest Science* reaches an international audience.

Members of the Northwest Scientific Association help support research and scholarship across a wide range of disciplines. Members also help underwrite scientific investigations through the Association's Research Grant Fund for graduate and undergraduate students. The annual meeting of the Association includes invited symposia as well as contributed paper sections.

Membership in the Northwest Scientific Association includes a subscription to *Northwest Science* and can be obtained by paying the appropriate dues (listed below). In addition to regular quarterly issues, members also receive occasional special issues focusing on particular scientific topics.

Inquiries concerning submissions for the journal should be directed to the Editor, whose address is listed in the inside front cover of the journal.

Clip and mail

I would like to join the Northwest Scientific Association and receive the quarterly publication *Northwest Science*.
Enclosed is a check or money order for membership dues for one year as a(n):

- ❑ Regular member ($25.00)
- ❑ Student member ($10.00)
- ❑ Institutional member ($40.00)
- ❑ Sustaining member ($40.00)
- ❑ Sustaining institutional member ($100.00)

Name

Address

City State/Province Postal Code

Dues are payable in advance and by calendar year. Please make all checks payable to the Northwest Scientific Association in U.S. currency and send to Northwest Science, c/o Washington State University Press, PO Box 645910, Pullman, WA 99164-5910, USA.

Honorary Life Members

Ewart M. Baldwin
L. C. Cady
Robert L. Carr
Bruce V. Ettling
William K. Ferrell
Nancy J. Grunewald
Philip Haddock
Kenneth Hammond
Adolph Hecht
Caroline Hooper
Kenneth V. Kardong
Denis P. Lavender
Lewis and Clark High School Library (In memory of Thomas Large and J. G. McCracken)
Joseph W. Mills
Richard J. Naskali
Frank D. Nicol
David L. Peterson
Oscar Sziklai
Robert F. Tarrant
Richard B. Walker
D. J. Wort

1998 Institutional Members

Boise State University, Boise, ID
British Columbia Institute of Technology, Burnaby, BC, Canada
Central Oregon Community College, Bend, OR
Central Washington University, Ellensburg, WA
Centralia College, Centralia, WA
College of Idaho, Caldwell, ID
Eastern Montana College, Billings, MT
Eastern Oregon State College, LaGrande, OR
Eastern Washington University, Cheney, WA
Edmonds Community College, Lynnwood, WA
The Evergreen State College, Olympia, WA
Grays Harbor College, Aberdeen, WA
Green River Community College, Auburn, WA
Idaho State University, Pocatello, ID
Lewis-Clark State College, Lewiston, ID
Lewis and Clark College, Portland, OR
Linfield College, McMinnville, OR
Montana College of MIning Science & Technology, Butte, MT
Mt. Hood Community College, Gresham, OR
North Idaho College, Coeur d'Alene, ID
Northern Montana College, Havre, MT
Oregon State University, Corvallis, OR
Pacific Lutheran University, Tacoma, WA
Pacific University, Forest Grove, OR
Peninsula College, Port Angeles, WA
Portland State University, Portland, OR
Simon Fraser University, Burnaby, BC, Canada
Skagit Valley College, Mount Vernon, WA
Spokane Falls Community College, Spokane, WA
University of Alaska, Fairbanks, AK
University of Alberta, Edmonton, AB, Canada
University of British Columbia, Vancouver, BC, Canada
University of Idaho, Moscow, ID
University of Montana, Missoula, MT
University of Oregon, Eugene, OR
University of Victoria, BC, Canada
University of Washington, Seattle, WA
Walla Walla College, College Place, WA
Washington State University, Pullman, WA
Western Washington University, Bellingham, WA
Whitman College, Walla Walla, WA

1998 Sustaining Individual Members

James K. Agee, Redmond, WA
Neil B. Armantrout, Eugene, OR
Donald J. Bedunah, Lolo, MT
Kevin R. Brown, Victoria, BC
Paul Carrara, Denver, CO
Richard A. Cellarius, Olympia, WA
Kermit Cromack,Jr., Corvallis, OR
Diane S. Doss, Sequim, WA
George W. Douglas, Duncan, BC
Larry A. Drew, Rathdrum, ID
Rich T. Easterly, Tenino, WA
Paul A. Fishman, Portland, OR
Robert W. Gray, Sumas, WA
Robert E. Gresswell, Corvallis, OR
Frederick C. Hall, Portland, OR
Paul E. Hammond, Portland, OR
Donald P. Hanley, Seattle, WA
David H. Hansen, Tacoma, WA
Randy Hein, East Wenatchee, WA
Jan A. Henderson, Mountlake Terrace, WA
Francis R. Herman, Fairbanks, AK
Barry L. Keller, Idaho Falls, ID
Karel Klinka, Richmond, BC
William N. Laval, Clarkston, WA
Giles W. Maloof, Boise, ID
Paul A. McDaniel, Moscow, ID
James A. McGee, East Wenatchee, WA
Howard R. Panik, Carson City, NV
Mauri S. Pelto, Dudley, MA
Steven K. Rust, Boise, ID
Penny Schaefer, Lacey, WA
Edward G. Schreiner, Port Angeles, WA
Charles G. Shaw, Auke Bay, AK
Dale Stradling, Cheney, WA
Kenneth C. Swedberg, Cheney, WA
Robert F. Tarrant, Corvallis, OR
Ted Thomas, Lacey, WA
David H. Wagner, Eugene, OR
James & Nancy Weber, Corvallis,OR
Andrea Woodward, Seattle, WA

Any member noticing information on this page that is outdated or incorrect should please bring this to the attention of the Editor.

WSU PRESS Washington State University Press
PO Box 645910
Pullman, Washington 99164-5910 USA

Nonprofit Organization
U.S. Postage
PAID
Pullman, WA
Permit No. 1

Northwest Science

Quarterly Publication of the Northwest Scientific Association

Papers published in **Northwest Science** are indexed in *Current Contents, Science Citation Index, Biological Abstracts, The Zoological Record, Recent Literature Supplement to The Auk, Abstracts in Anthropology, Bibliography and Index of Geology, Chemical Abstracts, Bibliography of Agriculture, Forestry Abstracts, University Microfilms, Geo Abstracts, GEOBASE,* and *Cambridge Scientific Abstracts, Elsevier BIOBASE/Current Awareness in Biological Sciences.*